STUDIES ON GREGARINES

Including Descriptions of Twenty-one New Species
and a Synopsis of the Eugregarine Records
from the Myriapoda, Coleoptera and
Orthoptera of the World

WITH FIFTEEN PLATES

BY

MINNIE ELIZABETH WATSON

THESIS

Submitted in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy in Zoology
in the Graduate School of the
University of Illinois
1915

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MINNIE ELIZABETH WATSON

Contributions from the
Zoological Laboratory of the University of Illinois under the direction of
Henry B. Ward No. 65

VITA

Minnie Elizabeth Watson was born December 8, 1886, at Fostoria, Michigan. She attended the graded and high schools of this village and also the high school at Flint, Michigan, graduating from the latter institution in 1903. She entered Olivet College in 1906 and graduated in 1909 with the degree of A. B. She then taught in the high schools of Rockville Centre and Oyster Bay, Long Island, New York, for three years. The summer of 1910 was spent in graduate work at Middlebury College (Vermont). In 1912-13 she was Assistant in Zoology in the University of Illinois, taking the M. S. degree in 1913.

The summers of 1911, 1912, 1913, and 1914 were spent in work at the Biological Laboratory of the Brooklyn Institute at Cold Spring Harbor, Long Island. During the years of 1913-1914 and 1914-1915 she has been a Fellow in Zoology in the University of Illinois.

During the period of graduate study she published the following papers:

Some New Gregarine Parasites from Arthropoda. Journal of Parasitology, Volume II, pages 27-36; 2 plates.

Three New Gregarines from Marine Crustacea. Journal of Parasitology, Volume II, pages 129-136; 1 plate.

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INTRODUCTION

The following pages contain results from the study of a number of species of gregarines found as parasites in various Orthoptera, Coleoptera, and Myriapoda during the past three years. The work was done chiefly in the zoological research laboratory of the University of Illinois, under the supervision of Professor Henry B. Ward. I am deeply indebted to Professor Ward for his direction and helpful suggestions throughout. Four of the species described were found and studied at the Biological Laboratory of the Brooklyn Institute, Cold Spring Harbor, Long Island, N. Y., and I wish to express my gratitude to Dr. C. B. Davenport for the opportunity of carrying on investigations at the Station. I wish also to thank Professor F. D. Barker, Professor H. B. Baker, and Mr. Elmer Shafer for kindly sending me material from which parasites were obtained.

The gregarines were studied in order to procure data in addition to that already known concerning (1) their biology including the habitat, relation to the host, seasonal distribution, and character of movement, (2) their modes of reproduction, and (3) their systematic position; twenty-two species are described for the first time while additional data is given for many more species. One result of the work was the compilation of a synopsis wherein are recorded in concise form the known facts concerning all the polycystid gregarines which literature records from the Orthoptera, Coleoptera, and Myriapoda of the world. A list was made of all the polcystid gregarines known, with their hosts, in order that species may not be recorded as new which have hitherto been discovered and that new species may not be given names which have already been used.

TECHNIC

The following method was used in studying the live parasites: The anterior and posterior extremities of the host are clipped off as close to the ends of the animal as possible and the alimentary tract is drawn out intact. It is then slit lengthwise with fine scissors, placed flat on a slide, and the masses of food and the parasites then teased out carefully to form a layer as thin and as nearly transparent as possible.

Distilled water and normal salt solution were found to be the best media in which to observe the live gregarines. Plasmolysis is slower with

the former, while the parasites remain motile longer in the latter. A minimum amount of water or salt solution is used and a cover slip placed over the material to prevent rapid evaporation. The animals are now in an unnatural medium and will disintegrate rather rapidly, so sketches of those which are to be measured must be made with the camera lucida as soon as possible, using a minimum amount of light and a power of the miscroscope of about 100 diameters. When the parasites are nearly transparent, as are those of the species inhabiting the Coccinellidæ, e. g., a drop of iodine-iodide solution will turn them brown and thus render them visible; a weak saffranin solution serves to bring out *in vivo* the nucleus and sometimes the longitudinal striations.

Although the parasites are best studied alive, some stained preparations are valuable. In order to preserve parasites in toto for future study, the intestine of the host is slit lengthwise and teased apart gently to loosen the food masses and the parasites. It is then dropped into the fixing solution and agitated gently when the free parasites will drop to the bottom of the dish. The best fixing agent is corrosive-sublimate solution to which has been added a trace of acetic acid; the precipitate is first washed with 50% alcohol and iodine, then with 70% and iodine, and the parasites preserved in 70% alcohol until needed. Picro-formol after Bouin was used in some instances with good results.

For staining in toto, two methods are advisable. The slide may be smeared with a very small amount of egg albumen, the animals dropped upon it from a capillary pipette and the preparation placed horizontally in a dish of 35% alcohol for about two minutes to coagulate the albumen. It may then be carried very gradually down the alcohols to a water solution of Ehrlich's hematoxylin or to a rather weak alcoholic solution of borax-carmine and in the latter instance counter-stained with picric acid. The alcohols and stains should be placed in flat dishes so that the slide may be kept horizontal and gradualy immersed and withdrawn from each solution to insure against loss of the parasites. Many grades of alcohol should be used and the parasites kept in each alcohol about fifteen minutes.

If the material is abundant, the parasites may be stained *en masse* in a small dish, since they settle to the bottom, but there is always considerable loss in the transfer of liquids.

When material is very scarce and all of the parasites must be kept, it is best to preserve simply in glycerine. Parasites from one host intestine can be placed on several slides. A weak mixture is made of glycerine and water and a very little of this used, the parasites being under observation under the microscope the while, for it is very easy to add too much glycerine and in an instant destroy all the material. The water is very gradually withdrawn by adding a little glycerine for several suc-

cessive days. A little safranin, erythrosin, or other stain may be added to the mixture and will be taken up by the parasites. The colored solution can be removed from the slide as the glycerine applications are made stronger.

The study of totos should be supplemented as far as possible with sections. In the instance of the small species not visible to the eye, sections afford the only means of studying the exact location in the host. The whole alimentary tract is fixed and sectioned intact. Sections must be cut very thin, about two micra for the smaller species. Ehrlich's hematoxylin has been found the most satisfactory stain; it may be used alone or counter-stained with either erythrosin or eosin. Sections reveal the relation of the young parasite to the host cell, whether attached by an epimerite or intercellular, the position of the free sporonts in relation to the cell walls, and various points in structure of the sporonts. By means of sections the position of the sporont can be determined, whether inside or outside of the alimentary tract or its appendages. If the parasite is able to bore through the walls of the intestine into the coelom, the actual burrowing process is often depicted in a series of sections; whether the pyloric cæeca are a seat of infection is also revealed in this manner.

PREVIOUS WORK ON GREGARINES

In 1903 Minchin adequately summarized the history of gregarines from the time of Redi, who in 1708 recorded the discovery of what was possibly a gregarine, through Dufour, who gave in 1828 the first authentic account of these forms and named the genus which he found *Gregarina*, up to the beginning of the present century.

Other historians of the gregarines have been Lankester, in 1863, Bütschli, in 1882, and Léger, in 1892.

Like all groups of which little is known, much of the literature of the gregarines is purely systematic in character. Since Minchin's synopsis was written in 1903, as well as previously, work on the gregarines has been chiefly systematic. Many new species, a dozen new genera, and a very few new families have been named in the last decade. The suborder Schizogregarinæ (Minchin) has received considerable attention from such workers as Léger and Duboscq, Fantham, Siedlecki, Dogeil, and Brasil, and they have described many new species from Crustacea, tracheate Arthropoda and Holothuroidea. A few new species have been described among the Eugregarinæ by European and South American workers, and in the United States Crawley, Hall, and Ellis have contributed considerable data concerning new species, all those in the last named country being parasitic in tracheate Arthropoda.

Lühe (1903) and Sokolow (1911 and 1912) have given particular attention to the physiology, morphology and reproduction of gregarines in general.

A LIST OF TERMS USED IN DESCRIBING GREGARINES

Association: The group formed by the attachment of two or more sporonts.

Biassociative: The adjective referring to an association of two sporonts attached by unlike ends.

Cephaline gregarine: One which possesses an epimerite at some stage in its life history.

Cephalont: A term applied to the young gregarine with an epimerite.

Cyst: The structureless covering secreted by the associated sporonts at the beginning of reproduction.

Deutomerite: The portion of a sporont which is preceded by the septum.

Ectoplasm: The outer zone of the body comprising the epicyte, sarcocyte and myocyte.

Endoplasm: The granular protoplasm found within the ectoplasm.

Epicyte: The thin, fragile, external layer of the ectoplasm.

Epimerite: The temporary or rarely permanent structure at the anterior end of the protomerite by which the young parasite is attached to the host cell. It is derived from the epicyte.

Isogametes: Gametes which are morphologically identical. Present in most gregarines.

Karyosome: A chromatic mass surrounded by plastin and contained within the nucleus. The young individuals possess a single karyosome which often buds off others as the animals increase in size.

Longitudinal striations: The very delicate ridges which are on the outside of the epicyte.

Myocyte: An hypothetical ectoplasmic layer consisting of the myonemes.

Myonemes: The network of contracile fibrillæ embedded in the periphery of the endocyte and running around the animal crosswise. They produce movement.

Octozoic Spore: A spore containing eight sporozoites.

Polycystid: A term applied to gregarines possessing a septum which divides the endocyte into regions. Infrequently more than one septum is present.

Primite: The first individual in an association of two or more sporonts.

Protomerite: The portion of a sporont which precedes the septum.

Pseudocyst: The residual protoplasm which after the spores are separated acquires a membranous wall, swells until the true cyst-wall bursts and allows the extrusion of the ripe spores.

Sarocyte: A middle layer of the ectoplasm.

Satellite: Any sporont in an association which is attached behind the primite. Generally there is but one, but sometimes several are attached in a cluster to the posterior end of the primite or, more generally, arranged linearly one behind the other.

Septum: The thin layer of sarocyte which separates the two portions of the sporont, the protomerite and the deutomerite.

Spore: The body into which the zygote develops after the acquisition of a resistant outer coating.

Spore duct: A tubular outgrowth from the cyst through which the spores are exuded when ripe.

Sporocyst: The covering or coverings of the spore.

Sporont: An adult gregarine living free in a cavity and deprived of its epimerite.

Sporozoite: One of the eight, more or less, small falciform bodies which are released when the spore walls are absorbed.

Trophozoite: The young parasite which is either entirely intercellular or attached to an epithelial cell of the host by an epimerite. Synonymous with cephalont.

Zygote: The body formed from the union of two gametes.

Part I BIOLOGY

THE HOSTS INFECTED

Gregarines infect only invertebrates and they have been reported from the following phyla: Coelenterata, Echinodermata, Platyhelminthes, Coelhelminthes (Archianellidæ, Gephyrea, Hirudinea, Annelida Polychæta and Oligochæta), Arthropoda, (Crustacea, Onycophora, Myriapoda, Hexapoda, and Arachnida), Mollusca and Chordata (Enteropneusta and Tunicata). Thus far the only groups below the vertebrates from which gregarines have not been reported are the phyla Rotifera, Porifera, and Protozoa, and the sub-phylum Leptocardii.

Partial List of Animals Examined for Gregarines

	Number examined	Number parasitized
Myriapoda		
Scutigera sp.	10	0
Scolopendra sp.	5	0
Scolopocryptops sexspinosus	10	2
Lithobius sp.	15	6
Geophilus sp.	15	0
Euryurus erythropygus	2	2
Callipus lactarius	24	20
Parajulus impressus	30	25
Polydesmus virginiensis	6	0
Spiribolus marginatus	6	0
Julus sp.	10	0
Hemiptera		
Reduvius sp.	10	0
Many unidentified		0
Diptera		
Musca domestica	10	0
Unidentified larvae	50	0
Neuroptera		
Damsel fly larvae	15	0
Dragon fly larvae	30	5
Lepidoptera		
Many unidentified larvae		0

Partial List of Animals Examined for Gregarines

	Number examined	Number parasitized
Mollusca		
Venus mercenaria	10	0
Mactra solidissima	5	0
Mya arenaria	10	0
Mytilus edulis	5	0
Modiola sp.	5	0
Pecten irradiens	10	0
Ostrea virginica	15	0
Crustacea		
Porcellio sp.	8	0
Oniscus asellus	30	0
Talorchestia longicornis	500	200
Orchestia agilis	50	2
Orchestia palustris	10	0
Balanus eburneus	5	0
Balanus balanoides	50	0
Panopeus sayii	10	0
Eupagurus bernhardi	25	0
Uca pugilator	50	40
Uca pugnax	20	15
Cancer irroratus	4	0
Platyonichus sp.	4	0
Libinia dubia	50	40
Libinia emarginata		
Annelida		
Nereis sp.	5	5
Amphitrite sp.	6	2
Enchytraeus abbidis	12	6
Heliodrilus caliginosus	6	6
Allobophora foetida	4	4
Lumbricus terrestris	3	3
Cerebratulus lacteus	4	0
Coleoptera		
Carabidae	25	3
Galuita janus	30	0
Helanotus fissilis	7	0
Hydrophilus triangulis	3	0
Pterostichus stygicus	10	4
Dytiscidae	25	0
Gyrinidae	15	0
Dinetus assimilis	5	0
Agabus semivittatus	4	0
Tenebrionidae	15	7

Partial List of Animals Examined for Gregarines

	Number examined	Number parasitized
Passalus cornutus	24	0
Elateridae	7	4
Coccinellidae	30	3
Coccinella sp.	10	3
Coccinella novemnotata	5	3
Amara angustata	5	5
Coptotomus interrogatus	7	5
Orthoptera		
Ceuthophilus stygius	15	8
Forficula auricularia	15	0
Ichnoptera pennsylvanica	10	4
Gryllus abbreviatus	200	150
Gryllus pennsylvanica	100	80
Melanoplus femur-rubrum	300	200
Melanoplus differentialis	50	10
Melanoplus acridiorum	5	5
Melanoplus bivitattus	10	6
Schistocerca americana	2	1
Dissosteira carolina	10	5
Encoptolophus sordidis	25	15
Arphia sulphurea	5	5
Hesperotettix pratensis	10	8

This list is incomplete for many animals were examined and not identified when parasites were not found. The numbers given above are approximate.

LOCALITIES REPRESENTED

The hosts from which the parasites described in this paper were taken occurred chiefly in and around Urbana, Illinois. Some were taken in New Jersey, many on Long Island, and the marine material from Long Island Sound; material was received from Haverford, Pa., Colorado Springs, Colo., and Lincoln, Neb., which afforded new data on the distribution of several species.

SEAT OF INFECTION

The most frequently observed location for the sporonts is the mid intestine of the host. The parasites are not found in the esophagus, crop, or rectum except when the infection is very heavy. The pyloric caeca are sometimes infected and parasites attached to the intestinal walls have been recovered in great numbers from the coelom of a very few insects. Cysts are often recovered from the mid intestine but usually from the rectum. They can be easily procured from the moistened feces of those species in which they are large enough and opaque enough to be distin-

guished with the eye. I have been able to procure them in this manner from the Acrididae.

Cross-sections of the host intestine reveal the fact that the sporonts lie close to the epithelial walls and are not scattered through the food masses. In the Myriapoda, they lie deeply seated between the lobes of the intestine where they are not easily dislodgd. Thus the parasites are in position to absorb the richly laden digestive juices just before the latter reach the villi, and are not in danger of being swept along to the exterior by the peristaltic movements in the intestine.

In the Acrididae sporonts and trophozoites are found in the pyloric caeca as well as in the intestine. In the Myriapoda the sporonts are able to bore through the walls of the intestine and have been found, though rarely, in the coelom. One species of the genus *Steinina* was found in a beetle in masses on the outside of the intestinal walls, projecting into the coelom.

At least one family, the Stenophoridae, is intercellular in development and the trophozoites are embedded in the intestinal walls of the host; in the Gregarinidae, however, one end only of the trophozoite is projected into the epithelial cell of the host.

SEASONAL VARIATION WITHIN THE HOST

Investigation of the seasonal variation of gregarines was confined to the Acrididae and the Gryllidae, of the order Orthoptera. It extended over a period of two years. Locusts were collected around Urbana from early spring until about June 20, and were then very generally parasitized but the number of parasites per host was small, averaging from one to ten. The nymphs of the Acrididae which hatch in the early spring were not infected in April but showed a slight infection when examined in June.

In the fall, observations were again made at Urbana and disclosed a considerable increase in parasitism. Nearly every locust examined was heavily infected, fifty parasites being an approximate minimum.

The same increase in the fall was found to be true of the gregarines in crickets. About fifty adults were examined at Urbana in June and it was found that only five or six were infected, and these with very few parasites. In the fall of the same year practically every cricket examined revealed a heavy infection.

Crickets were examined frequently throughout July and August of two successive summers at the Biological Laboratory, Cold Spring Harbor, L. I. The parasitism here steadily increased from sparse to heavy inside of two months. Conditions there were particularly favorable to the rapid increase. The crickets were collected on the Sand Spit, a long narrow peninsula separating the inner and outer harbors, and were taken

from under the flotsam and jetsam which is brought to the inside of the spit by the incoming tide. There are no waves on this inner beach to change appreciably the upper limits of the tidal zone and the crickets were undisturbed. The cricket population is large and flourishing because of the influx of organic debris. Thus the insects are confined to a restricted habitat and as cysts are produced and the spores scattered, the animals are reinfected over and over again.

A number of crickets were taken in August from debris along the shores of Northport Harbor and Huntington Beach, Long Island, and all were uninfected. Both these localities are part of the exposed shore of Long Island Sound. A number were taken inland at Arlington, New Jersey, and were also uninfected. Practically every cricket examined in the late summer at Cold Spring Harbor and at Oyster Bay (four miles distant) was infected. The only explanation which can be offered by the writer for these phenomena is that the spores, having once become established in restricted area, have not yet found the means of becoming scattered broadcast but reproduce themselves in enormous numbers in restricted localities.

RELATION OF PARASITE TO HOST TISSUE

The effect of the parasite on the host is a subject still under discussion. Very little actual investigation has been carried on in this field but it is one which offers many interesting problems in biological chemistry.

In the growing stages, the Eugregarine is either completely intercellular without an epimerite, or possesses an epimerite by which it is attached to the epitelial cells of the host intestine, this factor depending on the family to which it belongs. All the Acephalinae (including *Monocystis*) and some of the Cephalinae (e. g. the Stenophoridae and the genus *Frenzelina* of the Gregarinidae) are intercellular; most of the cephaline Eugregarinae are not, however, intercellular but possess epimerites which alone penetrate the host cells.

When the parasite is completely intercellular, the sporozoite penetrates the free end of the cell, works its way inward by ameboid movement (Léger and Duboscq, 1909) and comes to rest in the vicinity of the nucleus. The parasite at once begins to affect the nucleus, causing the breaking up and rearrangement of the chromatin into small more or less spherical bodies which react differently to the stain than do the normal nuclei. The cytoplasm also is affected chemically for it stains less deeply than the normal cell cytoplasm.

Siedlecki (1901) thinks these changes are due to a substance secreted by the parasite. Using *Monocystis ascidiae* for material, he found that the parasitized cell is at first greatly enlarged. The parasite within this enlarged cell then increases enormously in size so that the host cell and its

contents may be ten or more times the size of the normal epithelial cell; the parasite finally breaks out, for its rate of growth exceeds that of the epithelial cell, whereupon the latter shrinks and finally disappears, the adjoining cells gradually filling in the space left. The author says the chemical substance secreted by the parasite at first stimulates growth in the epithelial cell and later retards it, killing the cell, the parasite escaping after dissolution has set in. The normal excretion must be emptied into the cytoplasm of the epithelial cell of the host and may provoke changes therein but whether or not the cell is killed by the entrance of this foreign substance is a question. There is no other source of food for the parasite than by absorption from the cell which surrounds it, and it appears to the writer that the shrinking of the cell is due at least in part to the gradual withdrawal of its liquid content and the absorption of the latter by the contiguous parasite. How else the intercellular parasite grows is not easily explained. If the host cell is killed by toxins which are the excretory products of the parasite, the dead protoplasm is gradually used up as food for the growing organism. An animal is generally poisoned by its own excretory products; the gregarine would seem to be an exception unless it is possible that the host cell remains alive and throws off the excretions of the parasite along with its own.

Those parasites which are not intercellular possess epimerites by which they are attached to the free end of the epithelium of the host, the rest of the parasite lying in the lumen of the intestine.

Five questions may be asked in this connection: (1) Does the *epimerite* absorb food from the parasitized epithelial cell? (2) Does the epimerite absorb from the latter *all* the food that the gregarine receives? (3) Does the *epicyte* of the gregarine body absorb all the food from the lumen of the intestine, and the epimerite act only as a holdfast organ? (4) Is a toxic substance given out through the wall of the parasite into the lumen of the intestine which is absorbed by the parts of the epithelial cells nearest the surface?

Laveran and Mesnil (1900) state that in *Pyxinia frenzeli* the cell to which the parasite is attached at first greatly hypertrophies then atrophies and finally disappears completely about the time the cephalont is ready to discard the epimerite and live free in the intestine. The hypertrophy, they say, is due to an increase in the liquid content of the cell only, with a decrease in the density of its cytoplasm and nucleus. They do not attempt to give an explanation for the cause of the phenomenon.

Léger and Duboscq (1902) think this hypertrophy is only apparent and not real, for the penetration of the sporozoite into the cell irritates it so that the cell contracts in length at the same time increasing in width, the latter phenomenon giving rise to the idea that there is hyertrophy. They think the parasite absorbs the cell content through the epimerite

alone, and that constant and steady increase in the withdrawal of the cell sap accounts for the apparent atrophy.

Pyxinia mobuzzi (Léger and Duboscq, 1902) possesses a long tongue-like epimerite (Fig. 98) which extends longitudinally through the penetrated cell as far as the mesothelial layer of the intestine. The penetrated cell seems to be uninjured by this epimerite and the authors think the animal absorbs blood from the capillaries in the mesothelium by means of the epimerite.

The Dactylophoridae, e. g., *Nina gracilis* Grebnecki (Fig. 30), have epimerites with many long radices, which Léger and Duboscq (1902: 458) state penetrate at many places several adjoining cells and probably function as an apparatus for nutrition. Many genera, *Beloides, Pyxinia,* etc., have a long central style in the epimerite which punctures the cytoplasmic vacuoles and absorbs the cell sap directly.

Siedlecki (1901:98) says the long filaments from the epimerite of *Nina gracilis* penetrate into the epithelial layers between the cells and do not puncture the cells themselves, as Léger and Duboscq think.

Minchin (1912) says that the cytoplasm of the cell is absorbed by the parasite, which I infer to mean used as food, and that "when the cytozoic phase is past and the host cell exhausted, the parasite drops off, shedding its epimerite."

The present writer agrees with Léger and Duboscq and with Minchin that *there is absorption through the epimerite.* When a free cephalont is stained, its epimerite is seen to contain considerable endoplasm and not to be merely an ectoplasmic structure filled with sap. Moreover, stained sections of parasitized epithelium reveal the presence of attached cephalonts which are transparent or nearly so and which do not absorb the stain. Living material often contains large numbers of free cephalonts which contain but very little protoplasm or none whatever. These facts lead to the theory that the epicyte is not yet in physiological condition to absorb fluids from the intestine but that all such absorption takes place through the epimerite. Whether or not the epimerite possesses an epicyte of different structural character from that of the rest of the body is not known. It does, however, possess a very delicate, fragile, highly permeable layer susceptible to slight changes in osmotic pressure. The suggestion may be made that because the chemical constituency of the fluids in the lumen of the intestine and in the epithelial cells is obviously dissimilar, the parasite may or may not be able to absorb either of these fluids through the epicyte; and if they are absorbed may not be nourished by one of these ingested fluids. The fact that the epimerite often contains protoplasm while the rest of the cephalont is still transparent or nearly so and that the cephalont remains nearly transparent as long as the epimerite persists, leads to the theory that whereas at first all the ab-

sorption takes place through the epimerite, as the cephalont develops there occurs a gradual change in food from the predigested cell sap to the juices free in the intestinal tract as well as a transfer in its mode of absorbing these substances from the epimerite to the general epicyte of the body. The general epicyte of the body may be physiologically different when the cephalont is very young from that when it is nearly ready to discard the epimerite.

The third question: *Does the epicyte of the gregarine body absorb all the food from the lumen of the intestine and the epimerite only act as a holdfast?* has been answered above in the negative. There may come a time when maturity approaches and the epimerite is at the point of being discarded when the question may be answered in the affirmative; during the greater part of the cephalont life, however, the epicyte is probably ineffective in absorbing nourishment.

Is a toxic substance given out into the parasitized cell through the epimerite of the parasite? Siedlecki (1901:100) says the presence of the parasite within the cell *(Monocystis ascidiae)* incites hypertrophy, then atrophy, and that these phenomena are due to the chemical action of the parasite. In another species, however, *Nina gracilis,* which possesses numerous long protoplasmic filaments which penetrate deeply into the epithelium of the intestine, the author says of these threads

> "Tous ces changements provoques dans l'epithelium sont de nature purement méchanique."

He has observed changes in form and displacement of the cells but regards these as unallied to the hypertrophy and atrophy which is induced by chemical excitation.

Siedlecki finds in one instance a chemical effect excited by the presence of the parasite in or attached to a cell; in another species purely a mechanical affect; while Léger and Duboscq, as mentioned, believe the apparent hypertrophy due to mechanical irritation of the parasite upon the cell rather than to any toxin secreted by the parasite. Yet illustrations given by Léger and Duboscq to prove a mechanical effect indicate a different staining reaction in the case of many of the parasitized cells and a rearrangement of the chromatin in the nucleus unlike that in normal cells.

The last question is stated as follows: *Is a toxic substance given out through the epicyte of the parasite into the lumen which is absorbed by the parts of the epithelium nearest the surface?* It is often the case that the free end of the cell is shrivelled first. This end is nearest the hypothetical center of influence of the toxin which would be given out through the body of the parasite exposed in the lumen. It is also the end which is penetrated by the epimerite and the part naturally used as food first. The fact that the whole cell often reacts differently to the stain and not

the outer end only, and that the deep seated nucleus is affected by the very small parasite indicates the untenability of this theory as a cause of cellular reaction to the parasite.

A theory for the shrivelling of the parasitized cell may be derived from the facts of liquid pressure. The cell wall is normally under some pressure from within, due to turgor. When the cell is punctured by the sporozoite, some of the cell sap might ooze out. Most of the liquid content of the cell is, however, contained in vacuoles and not liable to be affected by the puncture. The viscid cytoplasm of the cell would probably be unable to find exit through the small opening. The puncture is as small as is the penetrating sporozoite and closed by the same. The parasite grows rapidly, enlarging the opening only as fast as the parasite grows. I have in no instance seen a section wherein the cell wall was torn by the growing animal, and in every instance the two fitted together tightly so as to form seemingly one layer at the neck of the epimerite. Thus the theory of loss of cell content by the oozing out through the puncture made is untenable.

MOVEMENT IN GREGARINES

Movement in Gregarines has probably been observed as long as the animals themselves. Dufour (1837:11) said

> "Leurs movements sont fort obscur et leur locomobilite est d'une lenteur extreme; cependant je les ai constates."

Siebold (1837:408) doubted that Gregarines were animals for he saw no movements. Kölliker (1848:32-3) described movement of the gliding type as

> "Eine langsam vorwärtschreitende Bewegung ohne sichtbare Contractionen der Leibeshülle."

He also noted the bending movement and describes it as follows:

> "Bewegung nach dieser oder jener Richtung durch mehr oder minder energische, auf verschiedene Weisen sich combinirende Zusammenschnürungen der Leibeshülle."

Kölliker did not attempt to explain the cause of these movements but he answered the question raised by Siebold "Are the Gregarines animals?" by describing the violent contractions seen in many of his new species, movements which only animals possess.

Leidy (1849:232) "detected movements of an animal character," and discovered the longitudinal striations of the epicyte which he thought were muscular in function.

Van Beneden (1872) discovered the network of transverse fibrillae which Schneider (1875:505) called the myocyte. Contractility of the

elements in this myocyte has since then been assigned as the basis for the bending movements of Gregarines.

The first explanation for the gliding movement was offered by Schewiakoff (1894) who supposed a gelatinous secretion from the posterior end of the body formed a stalk and that as the animal secreted new additions to this stalk it pushed itself forward by the same amount.

Porter (1897) probably without knowledge of Schewiakoff's theory proposed the following hypothesis:

> "It [locomotion] is a 'very slow movement of translation in a straight line' without any apparent contraction of the walls of the body. It is probably caused by a very slight undulatory motion of the under surface of the animal."

Crawley (1902:420; 1903:57), unaware of Porter's hypothesis, came to the same conclusion that an undulatory movement on the under side of the body is the basis for locomotion; and he disagreed with Schewiakoff's explanation.

My observations on movement in Gregarines have been chiefly confined to the species *Leidyana erratica* of the family Gregarinidae because of its activity and the readiness with which material is obtained.

In the normal intestinal juices of the host when the intestine is first opened, practically none of the animals are in motion; they lie rather in inert masses from which the name Gregarine is derived. Since the juices rapidly evaporate and cannot be secured from other animals in sufficient abundance to observe normal movement over a considerable portion of time, artificial media must be used, the most common being distilled water. This causes the animals to disintegrate after periods varying from fifteen minutes to three or four hours, depending on the age of the parasites and their consequent ability to adapt themselves to a change in external pressure. The young, fragile animals disintegrate rapidly; the oldest often resist the change in external pressure for several hours. When an epimerite is present on a free individual, it is quickly ruptured in water.

Egg albumen is not a satisfactory medium in which to observe motion, for the parasite has great difficulty in ploughing its way through the thick substance. Rupture of the walls is prevented by its use because of a similarity in density between the animal protoplasm and this medium.

Various acids in 0.5% solution were used and their effects on motion noted, among them being hydrochloric, nitric, acetic, sulphuric, and tannic. All of them killed the animals very quickly and caused the protoplasm to collect in masses; the epicyte was also often ruptured. Chloroform and sulphuric ether in 0.5% solutions produced no apparent structural changes but the parasites were quickly anesthetized.

Normal salt solution acts as a stimulant to motion and in it the parasites remain alive and active longer than in water. It is therefore the best medium in which to observe motion. Sea water has practically the same effect as normal saline.

Movement of location consists of a uniform gliding progression with no apparent localized motion of the body. It is best seen in animals from a freshly opened host intestine mounted on a slide and supplied with an abundance of light. The parasites are negatively heliotropic and consequently attempt to avoid the light rays by moving rapidly from the tissues toward the periphery of the cover slip and down the sides until they encounter masses of debris under which they try to hide.

The rate of progression has been measured in several instances. It averaged 0.8 micron per second in *Leidyana erratica*. The same individual is able to increase or decrease its rate of motion through a considerable range. A sample set of successive rates, measured at intervals of 15 seconds, reads as follows: 0.7, 1.8, 4, 5.6, 2.8, 1.5, 0.8, and 0.0 per second. An accompanying diagram (Fig. 233) illustrates progression combined with bending movement and the distances covered in successive time intervals. In the Stenophoridae motion of progression is slower, an average being .007 per second for two species, one of which was five times the length of the other and of correspondingly greater volume.

Just how the progressive movement is effected is a matter much discussed. Schewiakoff (1894) makes the statement that it is caused by the secretion of a hollow gelatinous "stalk" formed of contiguous threads at the posterior end of the body which pushes the animal forward. He says that the gregarine is able to move only until its store of secretion is exhausted and cannot go on until it has accumulated the materials from which to secrete a new addition to the "stalk".

Upon cutting off most of the light from the field, there can be seen many fine threads leading from the posterior end of the gregarine back to a mass of debris from which it is apparently trying to extricate itself. A slight motion of the microscope or of the table beneath will cause the threads to tremble; but even a slight movement of the cover slip does not rupture them. I have often observed the animal swinging about in an arc at the end of this fastened thread or strand of threads without breaking it. This was noted in twenty-five instances in a single field and was repeated by the parasites until their walls were ruptured and the protoplasm oozed out.

After a mount has been made for some time and the gregarines have become scattered about in the debris, many animals can often be seen headed away from inert masses, moving a short distance forward and then being jerked quickly back as if by some invisible spring. When an animal is able to free itself, the relase is sudden and the distance trav-

ersed often as great as the time it takes is short. The release may be compared to the cutting of a tense cord. Generally, however, the parasite is not able to effect its release and keeps on trying until the walls are ruptured or death ensues from some other cause.

I have never observed backward gliding movement. The only backward motion seen was the sudden jerking mentioned above. This phenomenon may possibly be accounted for in the following manner: The animal exerts considerable effort to move forward against the backward pull of the threads and debris behind it. Its body becomes stretched out long and narrow by the contraction of the myonemes. These myoneme fibrillae suddenly relax and the body becomes shorter and normal in shape. As the tension on the caudal threads is thus released, the body is drawn backward with a sudden jerk. The motion is thus passive, a simple reaction and not actively incited motion in a backward direction.

It is not to be denied, then, that there are formed gelatinous threads which seem to fuse and form a thick thread or strand from the posterior end of the body, but these threads are obviously an hindrance rather than an incentive to progression. My theory concerning the reason for the presence of such a group of threads will be discussed later.

Granted here that such a group is present, it obviously comes from the animal itself and is carried to the posterior end of the body by the longitudinal ridges which gregarines possess (see Fig. 243 for illustration of these longitudinal ridges). The animal in a mass of debris tries to liberate itself. In this motion there is secreted a lubricating substance which in a medium other than the normal digestive juices adheres to the debris. In endeavoring to get free, a great deal of energy is expended and considerable lubrication secreted; and thus the thread is formed from which the animal is unable to extricate itself. Each added trial only causes more secretion to be poured out and makes the snare the more secure. The body becomes drawn out long and slender indicating the strain which the animal undergoes (Fig. 236).

I suggest the hypothesis that normally there is a secretion which reaches the posterior end. When a parasite is moving through a medium in which there is fine scattered debris, it picks up much of it. After a considerable accumulation has taken place, one of two things may happen: The end masses may drop off by their own weight, the force exerted by the strand of threads being less than that exerted either by the progressing animal or by the dead weight behind. If the strand withstands the stress exerted by the moving animal but the dead weight exerts greater force than the combination of the other two, the strand and the animal, the parasite is caught and eventually dies.

The presence of the caudal threads can often be demonstrated with carmine. In a freshly made mount the carmine does not seem to adhere

and I have never been able to demonstrate the presence of threads in a freshly opened intestine. The medium must then be other than the normal digestive juices. It thus seems possible that no strands are present in the normal condition but that they harden only after being for some time in an unnatural medium. Instead of hardening and condensing in the host, the constituents of the secretion are probably dissolved in the digestive juices as fast as formed.

As the reason for the presence of the semi-gelatinous secretion from the body, I accept the view of Porter which states that movement is probably caused by a very slight undulatory motion of the under surface of the animal. Just as *Limax* moves forward by a slight ventral, and dorsally imperceptible, muscular movement in a vertical direction on an underlying surface the friction of which is caused by the secretion of a sticky mucus, the gregarine moves forward by imperceptible vertical movements in the myonemes on that side of the body which happens to be ventral at the time, friction being produced with the under surface by the exudation of mucus from the body. That there is a secretion from the whole body and not only from the posterior region is demonstrated by carmine which adheres in fine particles to all parts of the animal.

It was shown by Schewiakoff that there are tiny pores between the longitudinal ridges. These probably serve as exits for the secretion. The longitudinal ridges carry it backward and away after it has served its usefulness in effecting motion. The secretion is in the form of threads simply because it is constricted into narrow lines by passing backward between the tiny ridges. The threads are not necessarily continuous but may be often broken.

Thus I am of the opinion that the secretion at the posterior end of the body does not produce motion, but that it is a waste product by the time it has reached this end; it is likewise effective as shown above in inhibiting motion in an unnatural medium, as well as in producing it.

Besides the simple progressive movement, a twisting or bending movement is commonly observed. The body bends often with little or no change of position. This bending involves chiefly the anterior half of the deutomerite. The protomerite is turned from side to side like the head of a higher animal while the parasite is progressing from place to place. The protomerite, of itself, apears however to be incapable of movement and not the slightest change in form has been noticed. The region of greatest capacity for motion is the anterior end of the deutomerite. The endocyte of this region flows out into small pockets made in the elastic epicyte and as a group of two or three small outpushings is made on one side, close together, the protomerite falls to the opposite side. An outpushing of several small pockets just below the bent over

protomerite tends to straighten it; if half a dozen or more are formed in a circle around the anterior end of the deutomerite, the protomerite will sink into the central depression and often be obscured from sight.

The parasite is able to move through a place much narrower than the width of the body by the contraction and expansion of the epicyte, as in the instance of an amoeba.

Bending movement when the animal is out of its normal habitat may be due to external stimuli such as the endeavor to avoid light and the water medium. When in the normal habitat, the animal does not need to move about in search of food, there is no light to avoid, and the chief function of the bending movement when the parasite is in the intestine is probably the formation of a cyst. Two animals rotate about an imaginary axis coming closer and closer together by bending more and more, and finally form a perfect sphere (see Figures 234, 235 and 238). The formation of cysts by the use of normal saline occurred in twenty-five minutes. The salt solution was removed as soon as the cyst was completely formed and the cyst washed with distilled water. It developed to completion with the exudation of ripe spores. Cysts have, however, developed in but little longer time in distilled water.

SUMMARY

1. Normal salt solution is the best artificial medium in which to study motion.
2. Locomotion is effected by means of a progressive, gliding movement with no apparent localized motion of the body.
3. Progression takes place at the average rate of 0.8 per second in *Leidyana erratica*.
4. In artificial media there are formed gelatinous threads at the posterior end of the deutomerite.
5. These threads may be seen with a high power and a minimum amount of light in a mount which has been made for some time.
6. They do not occur in a freshly made mount.
7. The threads may be demonstrated with carmine granules in suspension.
8. The animal probably moves by imperceptible vertical movements of the myonemes of the side which is ventral at the time, and upon a surface whose friction is caused by an exudation of slime from the body of the parasite.
9. This mucus is secreted by the body and runs out through pores between the longitudinal ridges in the epicyte.

10. The mucus runs backward along the longitudinal ridges to the posterior end and is discharged as a waste product in the form of broken threads or strands.
11. The anterior half of the deutomerite is the region chiefly involved in bending movement.
12. The protomerite is incapable of independent bending movement.
13. The normal object of contortion is the formation of cysts.

PART II

MORPHOLOGY OF GREGARINES

MORPHOLOGY OF THE SPORONTS

The structural characteristics of the Gregarines have been described by many writers, including Delage and Hérouard (1896), Bütschli (1882), Minchin (1903, 1912), Doflein (1911), and others. For this reason I have not attempted to describe the general morphology of the group but rather to state facts of form and structure which I have observed in the two families under observation, viz., the Stenophoridae and the Gregarinidae.

The Stenophoridae

All of the species of this family are solitary. In all gregarines which reproduce sexually, the union of two sporonts is necessary but in the Stenophoridae this intimate association lasts only while the cyst is being made and not, as in some families, during the greater part of the sporont life. The cyst is probably formed quickly and this union very brief; no sporonts were seen in the process of cyst formation.

One characteristic of almost all the described Stenophoridae is the great length of the deutomerite as compared with the protomerite. The ratio is seldom less than 10:1 and is often as high as 30:1.

The protomerite is not constant in shape; it is, however, generally more or less conical, rounded at the apex, either as a simple cone (Fig. 7) or constricted or dilated slightly halfway from apex to base (Figs. 14, 16, etc.); there is generally, but not always, a small papilla at the anterior end (Fig. 24). The epimerite, which is superimposed upon the protomerite of the cephalont, contains some endoplasm which is continuous with that of the protomerite through the narrow neck connecting epimerite and protomerite. At the apex of the protomerite of the sporont, i. e., an individual which has lost its epimerite, the epicyte is very thin and the endocyte reaches nearly to the top. When the epicyte of the sporont upon the slide is ruptured, this rupture takes place at the apex and is accompanied by an extrusion of protoplasm at this point; the endocyte breaks first at its weakest place and in this family the apex of the protomerite is the weakest point. The thinness of the ectoplasm at

the apex gives rise to the idea that there is a pore here.* I am of the opinion that there is no pore but that the epimerite severs its connection with the trophozoite by gradual constriction at its short neck and drops off as a ball. The apex of the protomerite closes over completely, leaving a trace of the narrow channel in the epicyte by which the endoplasm of the two parts was in connection. That there is an opening to the exterior at this point in the sporont seems doubtful for I have never seen the extrusion of endoplasm in a freshly taken sporont to which slight pressure was applied; it occurred only when the animal had been kept on a slide in a normal saline or water medium, and then only after from fifteen minutes to an hour, or until the decrease in the density of the outside medium had had time to affect the parasite.

Not all protomerites of the Stenophoridae are conical in shape. In *Stenophora brölemanni* Léger and Duboscq (Fig. 13) the protomerite is shaped like a flattened cork fitting into the neck of a bottle, the deutomerite surrounding it in a thin layer nearly to the apex; in *Stenophora spiroboli* Crawley it is almost hemispherical in shape (Fig. 70).

In sporonts of the Stenophoridae I have seen, the deutomerite is long and slender. Léger and Duboscq record dimorphism in several species, *Stenophora silene* (Figs. 22, 23), *S. chordeume* (Figs. 24, 25), *S. varians* (Figs. 16, 17), etc., wherein the sporonts are both elongate and subglobular in shape. However, I have not observed an authentic and unquestionable case of dimorphism. The long, slender sporonts are, nevertheless, able to contract so as to be of quite a different shape from the normal. Immature specimens of several species are subglobular and stain more deeply than the sporonts but no mature subglobular specimens have been seen.

There is generally a constriction at the septum which distinctly differentiates protomerite and deutomerite; this is lacking in *Stenophora spiroboli* Crawley (Fig. 70) and in *S. robusta* Ellis (Fig. 26), and is only slightly developed in *S. polydesmi* (Lankester). The widest part of the deutomerite is generally the anterior third; sometimes the deutomerite is a cylinder more or less equal in width throughout. A combination of the two shapes is seen in *Stenophora diplocorpa* (Fig. 21), in which the deutomerite gradually broadens and then contracts in the anterior half, being conspicuously constricted at the middle and cylindrical posterior to the constriction. The deutomerite terminates in a broadly rounded, truncated, or conical extremity.

The protomerite and deutomerite differ greatly in endoplasmic content, and therefore in color and consistency. The protomerite is

*As stated by Ellis (1912b) in the Diplopoda.

always the less dense, being often nearly or quite transparent; the granular content is sparse and the large irregular granules are often clustered near the septum, the rest of the space being filled with a colorless fluid. The two parts differ in staining reactions also. The deutomerite contains fairly homogeneous endoplasm always densest at the center of the mass, which is generally in the anterior third of the body. In the posterior part of the attenuated forms, there is often so little endoplasm that the animal is transparent in the last fifth to third of its body. The deutomerite is generally gray or black in its densest regions and a lighter gray in regions of less density.

The nucleus may be either spherical or ellipsoidal in the sporonts, and varies considerably in relative size in different species. It generally contains one karyosome in mature sporonts of this family, sometimes more than one, but never many, and the karyosomes stain deeply, often revealing the presence of one or two very small centrioles within.

Longitudinal striations in the epicyte seem to be characteristic of the family, and myonemes have been observed in a great many instances. See figure 243 for these structures in *Leidyana erratica,* one of the Gregarinidae. It is probable that both types of structures are invariably present in motile gregarines and form the material foundation for prevailing ideas as to the cause of motion.

The epimerite seems to be an inconstant factor. Sometimes it is well developed and even retained in specimens free in the lumen of the intestine *(Stenaphora nematoides,* Fig. 15; *S. diplocorpa,* and *S. lactaria).* Generally, however, workers who have not sectioned the intestines of hosts have failed to find any trace of an epimerite. This is possible from the fact that development is intercellular and not extracellular as in the Gregarinidae, in which family the epimerite alone penetrates the cell. The whole trophozoite lies embedded and is able to obtain nourishment by osmosis, just as it does when it becomes a sporont, taking food in the former instance from the cell originally penetrated and those surrounding rather than from the lumen. Often intercellular parasites are found without epimerites (Léger and Duboscq, 1904, Pl. XIV, Figs. 1, 2, 4) and yet in the same section there may be smaller specimens which show the epimerite. The reason for the presence of an epimerite at all is not evident unless it is an ancestral vestige, for it disappears while the animal is still living an intercellular existence.

The larger embedded trophozoites are found in various positions in the host cells, generally, however, headed away from the lumen, i. e. with their protomerites contiguous with the mesothelial lining of the intestine. Infrequently one is met which has the protomerite turned toward the lumen (Léger and Duboscq, 1904, Fig. 6). Individuals of *Stenophora lactaria* have frequently been found boring their way, pro-

tomerite first, through the mesothelial walls of the intestine into the coelom, and in sections of the host some specimens have actually been found in the coelom lying close to the coelomic epithelium of the intestine. During the boring process the muscular tissue in the wake of the parasite is destroyed, leaving the surrounding tissue shredded and contorted.

The adult parasites seem to prefer lying loose between lobes or clusters of intestinal cells rather than living in the open lumen. The interstices of the lobes are very frequently occupied by large adult gregarines.

The sporozoite is spindle shaped and swells in the lumen. It penetrates the free end of a cell between the cilia and undergoes development within the cell. The first trophozoic stage I have seen is the small, completely formed body without a protomerite, lying embedded with its epimerite at the distal end of the cell next to the mesothelial layer. It undergoes considerable growth here with the consequence that the cell is destroyed and the parasite comes to lie in a self-formed cyst between two cells, often affecting parts of these cells and causing the cells for some distance around to be greatly compressed. Then the epimerite disappears and the protomerite develops and becomes more or less flattened against the basement layer of the cell. The trophozoites emerge into the lumen through the space left by the originally destroyed cell. The nucleus of the trophozoite of *Stenophora lactaria* is spherical; it begins however to acquire its ellipsoidal form while still in the intercellular stage.

The Gregarinidae

The parasites of this family become associative while they are quite immature and long before they are ready to form cysts. The shape of the sporonts remains fairly constant whether they are young or fully mature. The sporonts of the genus *Gregarina* are always more or less obese, and very frequently dolioform. The protomerite is much larger than in the Stenophoridae in comparison to the size of the body. In length, it varies from one-half to one-eighth the total length of the body. It is frequently hemispherical and as often cylindrical, rounded in front, but it is more than twice as high as wide; it is rarely conoidal. There is sometimes a slight indentation at the apex.

The epicyte is fairly thick throughout but is thicker at the anterior end of the body and at the septum than elsewhere.

The deutomerite is nearly always wider than the protomerite. It is fairly regular in shape throughout the family, being generally widest at the middle or slightly anterior thereto and gradually tapering both anteriorly and posteriorly. The posterior end is always rounded; it is never sharply acute.

The endoplasmic content of the protomerite and deutomerite differ more in density than in character of the granules. The protomerite contains homogeneous granules about the same size and consistency as those of the deutomerite but fewer in number, rendering this portion always less dense.

Myonemes are difficult to detect in the Gregarinidae, even with an oil immersion objective, when the animals are alive. They can be seen in longitudinal sections of adults as large deeply stained dots seemingly larger protoplasmic granules, situated at the edge of the endoplasm (Fig. 232). Cross sections naturally do not reveal their presence. In total mounts and with an intravitam stain they can be seen as a delicate network of fibrillae extending around the animal (Fig. 243).

Longitudinal striations in the epicyte are rendered visible by simply crushing the animal on the slide and liberating the dense endocyte. They are very delicate parallel striations visible with the oil immersion lens and situated on the outside of the epicyte. They may be seen in both protomerite and deutomerite and traced continuously from one end of the animal to the other (Fig. 243). They do not converge at the anterior and posterior ends, being continuous over the ends as at other parts of the body. The writer has never seen between the striations the pores which Schewiakoff says serve for the extrusion of the mucus.

The nucleus in the genus *Gregarina* is always spherical. In the trophozoites and in immature sporonts there is often but one large karyosome and never more than five or six. As the size of the animal increases, the karyosomes increase in number and decrease in size and are scattered irregularly throughout the nucleus. In mature sporonts they are often arranged in a twisted chaplet and are then too numerous to count. One of the reasons why maturity of the cyst and its dehiscence in the Gregarinidae occupies so short a time (two days) may be that the nucleus of the mature sporonts has already broken up into numerous small elements before cyst formation has taken place and only needs to lose its wall while in the cyst for these particles to surround themselves with a portion of the sporont endoplasm and becomes gametes. In the Stenophoridae, the nucleus of a mature sporont contains but one large karyosome which after cyst formation has taken place must break up into constituent elements.

The epimerite of all the Gregarinidae in which it has been observed is a large globular slightly stalked or sessile structure which is often retained after its usefulness is gone and the trophozoite is liberated in the lumen (Figs. 224 to 227). There is little endoplasm present in the nearly transparent epimerite which can be demonstrated with an intravitam stain.

LIFE HISTORY OF A TYPICAL CEPHALINE GREGARINE

The life history may be outlined briefly as follows: Sporozoite—trophozoite—sporont—gamete—zygote—spore—sporozoite. The sporozoite is a very minute falciform body liberated from the spore by the action of the digestive juices of the host which has swallowed it.* This small body apparently possesses no means of locomotion other than the extrusion of protoplasm. It lodges among the cilia of the intestinal epithelium and bores its way into the cell by ameboid movement. (Léger and Duboscq, 1909). Penetration is probably effected by the excretion of a toxin which lowers the resistance of the cell wall. It either merely punctures the wall and projects a small portion of its body into the cell, as in most Gregarinidae, or completely embeds itself in the cell mass, deriving its nourishment from the cell sap, as in the Stenophoridae. As soon as the sporozoite begins to absorb nourishment and to grow, it becomes a trophozoite. A combination of factors determines when the trophozoite shall be liberated into the lumen of the cell. The destruction of epithelial cells and the growth of the parasite go hand in hand and when the cells no longer supply sufficient nourishment or when the activity of the parasite causes it to release its hold, the trophozoite is liberated into the intestine and thenceforth absorbs nourishment from the fluids of that cavity.

After the cell has been destroyed and the parasite liberated, the epimerite is no longer useful and drops off. With the loss of the epimerite and change in habitat, the animal becomes a sporont. At some stage in sporont life, generally an early one, a member of the genus *Gregarina* attaches to one end of the body another sporont, the two forming an association. In genera in which the sporonts are solitary, attachment of two sporonts takes place just previous to cyst formation. Upon reaching a certain size or density or because of some unknown internal factor, the two sporonts rotate about a common axis and form a sphere. This spherical mass acquires a relatively thick gelatinous covering, the cyst, and leaves the body of the host with the feces. If it remains in a moist place for 48 hours, development proceeds as follows: The sporont nucleus breaks up into a myriad of small chromidial bodies, each small body acquiring a small amount of the residual protoplasm of the sporont. These nucleated particles are gametes. The gametes of the two sporonts are allowed to mingle by the beaking down of the separtion walls, when they fuse two by two and form zygotes. The zygote acquires a tough, resistant transparent covering and the content breaks up into eight parts,

*There is some evidence to substantiate the theory that autoinfection occurs and accounts for the enormous number of parasites which is often present in a host. See last page of section on cysts.

each with a portion of the zygote nucleus. The resulting body is an octozoic spore. The spores are liberated from the cyst through spore ducts which are formed from the residual protoplasm of the cyst. They are scattered over the grass and ground by the wind and rain and are eaten by some host along with its food. Parasitism is thus accidental. The spores upon reaching the alimentary canal of the host are acted upon by the digestive juices and the spore wall absorbed. Upon the disappearance of the wall, the eight sporozoites are set free and the life history starts on the same cycle again.

THE QUESTION OF SPORONT MATURITY

The question may be raised in connection with the development of the sporonts and cysts: Can one detect a sporont which is fully mature and ready for cyst formation? After many months of observation upon a number of species of several genera, I have come to the conclusion that full maturity can be detected and the imminent cyst formation predicted. In a genus like *Gregarina,* in which the association of sporonts is a characteristic feature, the fact that specimens are in associations of two does not indicate that the sporonts are mature, for associations are often formed early in sporont life while the animals are very small and obviously immature. In fact many sporonts are seen in association which are much smaller than some cephalonts of the same species free in the intestine. The fact that sporonts are linked together in twos is not an indication of maturity.

Density of the animals is often a criterion of maturity but not one upon which to depend. Cephalonts are transparent or nearly so; the small sporonts are but slightly opaque and opacity increases steadily with age, the oldest in many species being very dense and practically black in transmitted light. If, however, a host is starved a few days before being opened, the parasites are likewise starved and become more or less transparent.

Size increases with age and only the large individuals in any case may be expected soon to form cysts.

While no one of these three characteristics can be used as a test of maturity of the sporonts, an association of large sporonts in which the individuals are well filled with protoplasmic granules and hence opaque, indicates without doubt that the sporont is mature.

Movement of such an association is no longer the active motion of translation; the sporonts have become sluggish and tend to revolve. When the revolution becomes fairly well established, it takes a spiral form and gives place to rotation. The animals finally become a compact spherical mass with a cyst wall which has been secreted during rotation. The sporonts are now in position to reproduce themselves.

THE CYSTS

Observations on cyst formation and development, like those on movement have been confined chiefly to one species. In the Stenophoridae I have not been able to procure the dehiscence of any cysts; in the Gregarinidae observed, however, it was an easy matter to procure cysts and watch their development. Cysts were taken from moistened fecal masses or from the intestine by means of a needle and placed on slides. Bits of broken glass were used to raise the cover slip, and distilled water added. The cell was sealed with vaseline and placed in a petri dish well vaselined along the edges.

Cysts of the Stenophoridae observed were spherical or slightly ellipsoidal. They are generally found in the posterior part of the intestine and were not seen until fairly developed and rotation had ceased. It is not difficult to determine in most cases that two individuals were involved in making the cyst. The line of separation is often indicated in the cyst and there is often a slight difference in density of the two conjugants. In one instance one sporont was nearly black and the other pale tan. This fact was not noted until after the cyst had been in the damp chamber half an hour. In all cases observed the cysts became lighter in color after being in the damp chamber a few hours. In freshly opened intestines, cysts do not show a clear hyaline layer but after exposure the extrusion of water causes the inner mass to shrivel and the epicyst to swell so that the whole diameter is greater than at first. Although cysts were kept in the damp chamber nine days no spores developed. Whenever still intact, the cysts were crushed at the end of that time but there was no apparent differentiation of the protoplasm and none was revealed by staining. Most of the cysts were, however, shriveled and disintegrated.

Cyst Formation in the Gregarinidae—Leidyana erratica

This species is in its normal sporont stage non-associative. The young sporonts which have but recently lost their epimerites are nearly transparent but as age advances density increases, due to the absorption of food. The oldest sporonts are very dense and practically black in the deutomerite so that the nucleus is not visible when they are alive. The body in the young sporonts is long and rather slender, but it widens appreciably in the older ones. Middle-aged animals are very active in their movements but older ones are sluggish and tend to lie motionless in masses (Fig. 230).

In dense, sluggish individuals, one may expect cyst formation to take place. The sporont retains its power to bend and twist after it has apparently ceased to use its progressive powers. Sluggish individuals

in rotation set in motion currents in the surrounding medium and slowly attract into this ever-widening circle of influence particles of debris or nearby gregarines. If debris is drawn into the whirlpool, it is not retained, but slips to the outside again. Another gregarine is, however, attracted and held probably because of the mucus on its exterior, and caused to rotate with the first one. If two gregarines are attracted, the force exerted by the first is too weak to hold both and one is invariably liberated. A sporont is apparently unable to make a cyst alone. A single sporont has been seen to rotate for three hours without succeeding in attracting another and then to straighten out suddenly and move to another part of the field.

When such an association is formed, the sporonts are not attached by particular parts of the body, as are associations of the genus *Gregarina*, but are held together in a haphazard fashion by secretions only. In rotation the sporonts come closer and closer together laterally, slipping by a few sudden jerks until one does not project beyond the other, the protomerites bend around so as to meet the posterior ends of the deutomerites (Figs. 234 to 236), the deutomerites projecting and contracting so as to leave no unfilled interstices until the result is a compact sphere. In one such process, there was formed in the middle of one side of each deutomerite a tiny cupped indentation and the two cups fitted together to form a perfect sphere. This sphere became smaller and smaller as the cyst developed and finally disappeared in the general breaking down of the inclosed sporont walls (Figs. 235, 238).

The mass continues its slow rotation for hours. After a compact mass has been formed one can still distinguish the nuclei and the protomerite and deutomerite of each sporont, the former by the pale tan color (Figs. 239, 240). This demarcation is lost and soon after the faintly visible lighter nuclear areas disappear. The straight line which separates the two sporonts (their lateral walls) remains visible for twenty-four hours after the cyst has begun to form. It disappears finally and the cyst-mass becomes perfectly homogeneous throughout (Fig. 241).

All the time the mass is revolving there is being exuded from the two bodies the sticky, gelatinous, transparent secretion. This exudation follows the animals as very slender spiral threads and forms a spirally arranged layer constantly increasing in width as rotation continues. When rotation ceases there is formed around the cyst-mass an appreciable layer of this gelatinous matter arranged as very fine concentric threads.

Motion of the mass was watched in one instance to completion. My notes opposite the time of each successive complete rotation read as follows: "Brings another gregarine into the vortex; the two rotate together; shoves a third gregarine out of the way; retracts same; the two

slip and slide until they form a perfect sphere; central spherical area left between the two sporonts; gelatinous layer forming around the rotating sphere;the outer layer wider and distinct." The time for the first complete rotation of the solitary individual was one and one-eighth minutes. Approximately this rate is retained during sixteen rotations. The rotations then becomes slower as the mass more and more nearly approximates a sphere. Two and one-half minutes, four minutes, and five minutes are recorded for successive rotations. At the end of forty-five minutes the cyst was complete but still slowly rotated at the rate of one rotation in from four to five minutes. When next observed, two hours later, motion had ceased and there was present a gelatinous layer in thickness one-third the radius of the cyst.

Fully formed cysts which are still in the process of rotation were frequently taken from the host and they continue to rotate a half hour or more after removal.

Cyst Development and Dehiscence

When the mass has finished rotating, it is a beautifully homogeneous, opaque, gray spherule surrounded by a thick, transparent, cyst wall fifty micra in thickness or half the radius of the inner mass. The mass begins to disintegrate in twelve to fifteen hours, the protoplasm becoming arranged in many dense areas (Fig. 242). The diameter of the inner mass decreases and that of the transparent cyst wall increases by the exudation of water from the inner regions. In twenty-four hours the protoplasm within the cyst wall has begun to shrink from the periphery. Five hours later (29 hrs.) the spore ducts are clearly indicated (Fig. 245) by dense accumulations of protoplasm on the periphery or orange colored discs on the cyst surface. From three or four to a dozen of these discs are delineated. The orange color is due to an accumulation of orange colored oil which dissolves and loses its color in ether. Soudan III stains it red. The oil can be pressed out from the cyst in large globules. The origin of this oil in the cyst is, of course, the endoplasm of the sporonts. The protomerite is tan in color and probably contains considerable oil; the deutomerite may contain as much or more but the color is obscured by the great number of protoplasmic granules which render the whole very opaque.

After thirty-five hours, the ducts leading from the periphery to the center of the cyst mass appear; they resemble the spokes of a wheel. In a few more hours the spore ducts begin to project from the surface of the sphere; the center is depressed (Figs. 247, 248). By this time the individual spores are visible within the mass (Fig. 246). At the end of from forty-two to sixty hours, the spores are liberated (Fig. 249). Although from one to a dozen spore ducts begin to grow outward, not more than

one has been seen to complete itself. This is accounted for probably by the fact that pressure is exerted on most of the incipient ducts by the slide and cover slip, and growth to completion thus inhibited. One duct is often directed horizontally between the two surfaces and it always is this lateral duct which develops and through which spores are extruded. When there is considerable debris in the vicinity of the developing cysts, the ducts are often coiled and twisted about the cyst itself. I have never been able to incite spore exudation without the use of a cover slip for even in a carefully sealed damp chamber there is enough volume within the chamber to cause sufficient evaporation to dry up the unprotected cyst.

The duct which is formed is very long, 25 mm. or eight times the radius of the cyst (Fig. 249). The ducts grow inward from the periphery where they first appear to the region of the residual mass of protoplasm. Then they grow outward from the periphery until they acquire the enormous length attained in a few species. The growth outward is from the region of the periphery, the older portion being pushed ahead. The tip of the long duct is orange colored as is the disc from which growth began, showing that the oil globules are pushed along with the first outpushing of the tube. There does not seem to be an eversion of the duct here, as in *Gregarina rigida* and other species (Lankester, 1903:183).

The spores emerge in chains which soon break up into small segments. These spores (Fig. 255) are barrel-shaped and truncate at the ends. They possess an epispore and endospore easily discernible when a stain is used on the slide. They are slightly cupped at the ends. I think there is a corona of very delicate spines or cilia at each end which serves to hold the spores together in chains and to furnish a means of locomotion for the isolated spores. That spores do move from place to place is easily determined by watching a few chains of freshly liberated spores on a slide. (Care should be taken that the slide is undisturbed and not allowed to evaporate). In a few hours no two spores will be left attached but they will lie in small clusters or scattered over a whole field.

Sometimes spore ducts do not develop and the cyst has superficially undergone but little differentiation, yet upon crushing the walls after a day or so when the spore ducts should have been formed, perfectly formed spores emerge, to all appearances and staining reactions identical with those liberated in the usual way. Nothing could be said of their potency as compared with those extruded normally.

The content of the spores varies greatly. If the cyst is broken before the spore ducts have had a chance to form, and apparently before the spores are ripe, they will be found to contain many small clustered or isolated chromosomes which stain deeply. All the spores from a given cyst are in approximately the same stage of development. Another broken cyst will yield spores with fewer chromosomes, from ten to fif-

teen, for instance. A cyst brought to completion yielded spores in which each of the many examined contained eight large chromosomes. These spores were watched for a day and at the end of the twenty-four hours delicate partitions were seen, between each two of which was contained one large chromidial body. These partitions represented lines of separation between the eight sporozoites which were being developed (Fig. 255). I was unable to procure or find any liberated sporozoites by any of the following methods: 1) Some spores were left on the slide in a water medium; 2) others were placed in normal sodium chloride solution; 3) the intestinal juice of a freshly killed cricket was run under a third cover slip on which were a few spores; and 4) spores were placed on a small mass of fresh intestinal epithelium. In the last two instances putrefaction was soon set up in the non-sterile tissues. Using spores of another gregarine *(Frenzelina delphinia)* from a crab, I sterilized some of the colorless blood from the heart of the crab by boiling it in a test tube and used the liquid as a medium but without inciting spore development.

Cysts were crushed at various developmental stages and stained. The spores were found to be well developed before the spore ducts were formed, so the early stages of development are the sources of greatest changes.

Immediately after the protoplasm of the cyst becomes collected in masses, small clear papillae begin to appear on the periphery of each mottled mass (Fig. 244). The layer of papillae being formed, another develops beneath, until the three or four outer layers of the cyst show these papillae, the inner mass being residual non-metamorphosed protoplasm.

The papillae soon become pinched off to form tiny globular bodies, each of which contains a deeply staining particle inside. These globular bodies are the gametes (Fig. 251). Upon crushing and staining a cyst in the gamete stage, I have repeatedly been unable to find the least evidence of a difference in shape or size or in staining reaction between the gametes from opposite poles of the cyst; i. e., from each of the two constituent sporonts. The gametes are isogametes. That there is, however, a difference between them is shown by the attraction of certain gametes for others. Before the partition wall between the two sporonts is absorbed, the gametes of each side do not attract others from the same side of the partition. But when the partition wall has dissolved and the cyst is examined, it is seen to contain many 'double' gametes; i. e., gametes united in pairs (Fig. 252). If taken early enough, the gametes are seen to be barely contiguous at one point. The next stage observed is that in which each retains its identity but is flattened on the side of attachment to the other (Fig. 253). Then the identity of each becomes

lost and the result is a body twice the size of the original gamete, with a nuclear content made up of the fusion of that of the two gametes. This larger body, which in staining reaction is identical with that of the gametes, is the zygote. In a cyst of twenty-four hours, no spore ducts had begun to appear but the cyst was full of zygotes.

The zygotes when fully formed are ellipsoidal in shape, contain many small deeply staining bodies, and possess a rather thin wall (Fig. 234). They develop gradually into spores. The outline becomes more spore-like by the gradual flattening of the ends and the decrease in the number of chromidia while the outer wall increases in thickness. In a cyst of about thirty hours the zygotes have attained the shape of the ripe spores but the content is still that characteristic of the zygote.

From the thirtieth hour on, the chromidia rearrange themselves and decrease in number by fusion, and the perfection of the mechanism for expelling the ripe spores proceeds.

It is probable that the cyst can develop and spores be expelled while within the intestine, possibly resulting in the reinfection of the host and accounting for the enormous numbers of parasites found in some hosts. I have seen cysts dense and opaque, cysts pearl gray and mottled, and even cysts with spore ducts well developed and nine in number, all within the body of a freshly caught cricket. The same advanced stages of the cysts of another species have been found in the bodies of freshly opened locusts and also in certain Crustacea.

PART III

Synopsis of the Eugregarine Records of the Myriapoda, Coleoptera, and Orthoptera of the World

INTRODUCTION

The synopsis and list of parasites which follow were made in order to obtain the essential features of all the known species of eugregarines parasitic in three groups of animals so that in placing on record some twenty odd species which I had found during the last year there would be no danger of redescribing a species under a new name or of describing a new species under a name already used. It is hoped that the synopsis will be useful to future workers.

Species have been included from the whole world and not from the United States only, for many species of protozoa are notably cosmopolitan and not restricted to definite areas. The study of gregarines is as yet scarcely begun in the United States and very few species have been found both in the Old World and in the New, but workers in the United States must be on the lookout for Old World species and should not describe forms new to this country as actually new species without considering the parasites of other regions of the world.

Every effort has been made to include in the synopsis all the species mentioned in the literature. Sources of information are as follows: Dufour (1837), Kölliker (1848), Stein (1848), Frantzius (1848), Diesing (1851), Lankester (1863), Minchin (1903), Labbé (1899), Sokolow (1911), Ellis (1913b), indices of the Zoologischer Anzeiger from 1878 to 1895, cards of the Concilium Bibliographicum from 1895 to date, and current periodicals: Archiv für Protistenkunde, Archives de parasitologie, etc., for the past and present calendar years. To a great extent these references have acted as checks on each other although the original sources have not infrequently revealed other species not elsewhere mentioned. Many of the older species recorded in this synopsis do not appear in Labbé's Sporozoa.

Labbé repeatedly regards as synonyms species which occurred in the same host genus or in allied genera without regard to whether or not the species of parasites were identical. In most instances the species are

not the same although the same species or genus of host is involved; such unlike parasites have been separated. For example, *Phialoides ornata* Leger and *Gregarina brevirostra* Kölliker were regarded as synonymous because they infect the same host. In some instances Labbé regarded as synonymous species which actually belong together; for example, *Actinocephalus lucanus* Stein and *Stephanophora radiosa* Léger, which are identical, the species now being known as *Actinocephalus conicus* (Dufour) Stein.

The law of priority has been adhered to strictly and many parasites known by later assigned names have been referred to names given to them many years before, e. g. *Actinocephalus conicus* which was long known as *Actinocephalus lucanus*. Labbé in most instances calls such species by the later assigned names in his treatise.

In the descriptions of species, well developed sporonts have been taken as the standard except where such have not been described, these rare instances being noted in the synopsis. Shape of the cephalonts is often quite unlike that of the sporonts and thus of no systematic value in diagnosis. Whenever the epimerite is not mentioned in the literature, as is often the case, the generic determination of the author is based on other characters. The sporonts are often polymorphic and the synopsis records are based on expanded, quiescent, and, as far as known, normal specimens except where the polymorphism is marked. In these instances such facts are noted.

In the description of each new species, I have given measurements of only a few large, typical sporonts. These are taken from records of the measurements in most instances of twenty-five or more animals. In most published descriptions the length and width of one sporont only is stated, generally of the largest one observed and the ratios of various parts are based on this one parasite.

As the discovery of new species proceeds, I am of the opinion that many will be very similar to others already described and not easily differentiated from them unless a wide range of measurements and ratios is taken from parasites in different hosts and selections made therefrom for use as a table. This applies in particular to the genus *Gregarina*, where differences between species appear to be limited. One observer might find the maximum length to be a and the ratio of the two parts as 1:2. Another worker on the same species might find his largest specimen to be $2a$ long and the ratio of parts as 1:3 and describe the species as different from the former. A table showing lengths and ratios selected from measurements of many parasites in the same host and from as many hosts and under as varying conditions as possible (habitat, season, etc.) eliminates the danger of duplication of species.

I have differentiated new species in the same genus by the following

characteristics: Size, both medium and average; ratio of length of protomerite to total length; ratio of width of protomerite to width of deutomerite; general shape of the body; shape of the protomerite; shape of the deutomerite; character of the interlocking device; size and shape of the nucleus; color and character of the protoplasm; and the size and shape of the cysts and their method of dehiscence.

It is true of many species that the family or generic determination or both are uncertain because important diagnostic features such as the epimerite and spores are often lacking. The correct family can sometimes be determined when only one of these factors is present. In some instances the correct genus can be ascribed even though important data are lacking, e. g. the genus *Gregarina,* by its biassociative factor and the host involved. If there is any doubt about the position of a given animal, the parasite is placed at the end of the particular genus to which it may belong.

In describing the associative gregarines, generally only specific measurements of the primite are given for the proportions of satellite differ considerably within the same species as it happens to be more or less flattened while those of the primite remain fairly constant. The shape given for the posterior end of the deutomerite is that of the satellite, where the deutomerite is free at its posterior end; in the primite it is altered by contiguity with the protomerite of the primite.

The species of gregarines indigeneous to each of the three groups are arranged in families, and under each family the genera are placed in alphabetical order. In each genus the species are arranged in chronological order, the oldest first, the latest additions last. New species not hitherto found are described in detail in the groups to which their hosts belong.

In as many instances as possible, the names of the hosts have been checked and corrected to accord with the best authorities. However, this has often been impossible and the names had to be left as in the original citation. Especially is this true of the older species of parasites, many of which have not been found since the original discovery seventy-five years or more ago.

The names of the Myriapod hosts have been corrected, those abroad in accordance with Latzel (1884) and those endemic to the United States after Bollman (1893). Coleopteran literature seems not to be in condition to warrant the finding of synonyms for many of the early described species. For instance, the name by which a beetle is known today will be recorded, but not the name by which it was known some fifty years ago and by which it was called when the parasites infesting it were described. When names have been corrected to accord with present day

knowledge, the older name is placed in parenthesis after the now accepted name.

The spelling of the name of the diplopod *Julus* as given by Linnaeus (1766) has been used thruout wherever the word appears, whether in the name of the host or in the name of a species of parasite where the name is used as a prefix. The *Iulus* of some authors is, then, disregarded in the nomenclature of the species.

A Brief Synopsis of the Families and Genera of the Tribe Cephalina (Delage) of the Suborder Eugregarinae (Léger)

This synopsis is based on the classification of Minchin (1903, 1912) and Poche (1913).

Subphylum Sporozoa Leuckart 1879:241.

Class 1. Telosporidia Schaudinn. Sporulation ends the life of the individual.

Order 1. Gregarinida Bütschli 1882:503. Reproduction by spore formation only or by both spore formation and budding.

Suborder 1. Schizogregarinae Léger.

2. Eugregarinae Léger. Reproduction limited to spore formation. Spores octozoic.

Tribe 1. Acephalinae Kölliker (Monocystoidae Poche).

2. Cephalinae Delage 1896:269. Eugregarinae with an epimerite at some stage in the life history. Body usually divided by septum into protomerite and deutomerite. Spores with two coats. Mainly parasitic in the gut of arthropods.

Family 1. Didymophyidae Léger 1892:105. In associations of two or three. No septa in satellites.

Genus 1. Didymophyes Stein 1848:186. Characters of the family. Epimerite a small pointed papilla, cyst dehiscence by simple rupture. Spores ellipsoidal.

Family 2. Gregarinidae Labbé 1899:9. Associative or solitary, satellite with septum. Epimerite symmetrical, simple. Cysts with or without spore ducts.

Genus 2. Gregarina Dufour 1828:366. Biassociative. Epimerite small, globular or cylindrical. Spores dolioform to cylindrical. Cysts dehisce by spore ducts.

Genus 3. Hirmocystis Labbé 1899:12. Associations of from two to twelve or more. Epimerite a small cylindrical papilla. Cysts dehisce by simple rupture. Spores ovoidal.

Genus 4. Hyalospora Schneider 1875:583. Biassociative. Epimerite a simple globular knob. Cysts dehisce by simple rupture. Spores ellipsoidal. Endoplasm yellow-orange.

Genus 5. Cnemidospora Schneider 1882:446. Solitary. Epimerite not known. Anterior half of protomerite gray, posterior half yellow-green. Dehiscence of cysts by simple rupture. Spores ellipsoidal.

Genus 6. Euspora Schneider 1875:582. Biassociative. Epimerite not known. Cysts dehisce by simple rupture. Spores prismatic.

Genus 7. Sphaerocystis Léger 1892:115. Protomerite only in young stages. Solitary, subspherical. Dehiscence by simple rupture. Spores ovoidal.

Genus 8. Gamocystis Schneider 1875:587. Protomerite only in young stages. Associative. Sporulation partial, with spore ducts. Spores cylindrical.

Genus 9. Frenzelina Léger and Duboscq 1907:773. (Cephaloidophora Mawrodiadi 1908:101). Biassociative. Epimerite not known. Cysts dehisce by simple rupture. Spores ovoidal, with dark equatorial line. Intercellular development.

Genus 10. Uradiophora Mercier 1912:198. Bi- or triassociative. Epimerite simple style, forked at end. Cysts dehisce by simple rupture. Spores dolioform.

Genus 11. Leidyana Watson 1915. Solitary. Epimerite a simple globular sessile knob. Dehiscence by spore ducts. Spores dolioform.

Family 3. Dactylophoridae Léger 1892:165. Epimerite complex. Sporonts solitary. Cysts dehisce with lateral pseudocyst or by simple rupture. Spores elongate, cylindrical or ellipsoidal.

Genus 12. Dactylophorus Balbiani 1889:41. Protomerite dilated laterally with peripheral digitiform processes. Sporonts solitary. Spores in chains obliquely.

Genus 13. Nina Grebnecki 1873:—. Protomerite formed of two long narrow horizontal lobes fused and upturned spirally at one end. Periphery set with teeth from which project long slender filaments. Spores in chains obliquely.

Genus 14. Trichorhynchus Schneider 1882:438. Epimerite a very long slender neck with dilation on surface. Lateral pseudocyst for dehiscence. Spores cylindrical or ellipsoidal, not in chains.

Genus 15. Echinomera Labbé 1899:16. Epimerite an eccentric cone with eight or more short digitiform processes from sides. Dehiscence by simple rupture. Spores cylindrical, in chains.

Genus 16. Rhopalonia Léger 1893:1285. No protomerite in sporonts. Epimerite a subspherical cushion with ten or more short thick digitiform processes. Pseudocyst. Spores cylindrical.

Genus 17. Acutispora Crawley 1903:632. Epimerite not seen. Pseudocyst. Spores biconical, thick blunt endosporic rod at each end.

Genus 18. Metamera Duke 1910:261. Epimerite subconical, apex eccentric, surrounded by numerous branched digitiform appendages. Dehiscence by simple rupture. Spores biconical.

Family 4. Actinocephalidae Léger 1892:166. Sporonts solitary. Epimerites varied. Cysts dehisce by simple rupture. Spores irregular, biconical or cylindro-biconical.

Genus 19. Actinocephalus Stein 1848:196. Epimerite small, sessile or on a short neck, with 8 or 10 short sharp spines or simple bifurcate digitiform processes. Spores biconical.

Genus 20. Geneiorhynchus Schneider 1875:594. Epimerite a tuft of short bristles set at the apex of a long slender neck. Spores cylindro-biconical.

Genus 21. Pyxinia Hammerschmidt 1838:357. Epimerite a flat crenulate crateriform disc from center of which rises a short or long style. Spores biconical.

Genus 22. Beloides Labbé 1899:27. Epimerite a spiny globule with a long apical style set on a short stout neck. Spores biconical.

Genus 23. Phialoides Labbé 1899:24. Epimerite a broad cushion with peripheral row of teeth and a thickened collar placed on a long slender neck. Spores biconical.

Genus 24. Legeria Labbé 1899:24. Epimerite not known. Protomerite dilated and massive. Septum convex upward. Spores cylindro-conical.

Genus 25. Coleorhynchus Labbé 1899:23. Epimerite not known. Protomerite a round shallow disc depressed in center. Septum convex upward. Spores biconical.

Genus 26. Bothriopsis Schneider 1875:596. Epimerite an ovoidal structure with 6 or more long slender filaments. Protomerite very large, septum convex upward. Spores biconical.

Genus 27. Asterophora Léger 1892:129. Epimerite a thick horizontal disc with a milled border and a stout style projecting from center. Spores cylindro-biconical.

Genus 28. Schneideria Léger 1892:153. (Rhabdocystis Boldt 1910:289). Epimerite like that of Asterophora. Style shorter, no protomerite in sporonts. Spores biconical.

Genus 29. Stictospora Léger 1893:129. Epimerite spherical, centrally depressed, armed with a dozen backwardly directed mucrones set on a short neck. Spores biconical, slightly curved.

Genus 30. Stylocystis Léger 1899:526. Epimerite a recurved sharply pointed cone. Spores biconical.

Genus 31. Steinina Léger and Duboscq 1914:352. Epimerite a short mobile digitiform process changing into a flattened button. Spores biconical.

Genus 32. Taeniocystis Léger 1906:307. Epimerite a small sphere set with 6 or 8 recurved hooks. Deutomerite divided by septa into numerous linear segments. Spores biconical.

Genus 33. Discorhynchus Labbé 1899:20. (Sycia Léger 1892:52). Epimerite a large globular structure with a thin collar around base. Short stalk. Spores biconical, slightly curved.

Genus 34. Amphoroides Labbé 1899:20. Epimerite a globular sessile papilla. Protomerite cup shaped. Spores curved.

Genus 35. Pileocephalus Schneider 1875:591. Epimerite a lance-shaped or simple cone. Spores biconical.

Genus 36. Anthorhynchus Labbé 1899:19. Epimerite a large fluted flattened button. Spores ovoidal, pointed.

Genus 37. Sciadophora Léger 1899:18. Epimerite large, compressed laterally, peripherally crenulate. Protomerite bears numerous backwardly directed mucrones. Spores biconical.

Genus 38. Hoplorhynchus Carus 1863:570. Epimerite a flat button with 8 or 10 digitiform processes carried on a long collar. Spores biconical.

Genus 39. Amphorocephalus Ellis 1913:462. Epimerite dilated in middle, terminating in concave peripherally fluted disc at anterior end. Spores not known. Protomerite constricted across middle.

Family 5. Acanthosporidae Léger 1892:167. Sporonts solitary, epimerite simple or appendicular. Dehiscence by simple rupture. Spores with equatorial and polar spines.

Genus 40. Acanthospora Léger 1892:145. Epimerite a simple conical papilla. Spores biconical or ovoidal with row of equatorial spines and a tuft of four spines at each pole.

Genus 41. Corycella Léger 1892:144. Epimerite globular with 8 large recurved hooks. Spores biconical, 4 spines at each pole.

Genus 42. Ancyrophora Léger 1892:146. Epimerite a globule with 5 or 10 backwardly directed digitiform processes. Spores biconical with equatorial and polar spines.

Genus 43. Cometoides Labbé 1899:29. Epimerite a spherical button with long slender filaments. Spores cylindro-biconical, with polar and two rows of equatorial spines.

Family 6. Menosporidae Léger 1892:168. Sporonts solitary. Epimerite a large cup bordered with hooks and placed on a long slender collar. Cysts dehisce by simple rupture. Spores crescentic, smooth.

Genus 44. Menospora Léger 1892:168. Characters of the family.

Family 7. Stylocephalidae Ellis 1912:25. Sporonts solitary, epimerites varied. Nucleus ovoidal. Dehiscence by pseudocyst. Spores irregularly shaped, brown or black, in chains.

Genus 45. Stylocephalus Ellis 1912:25. Epimerite a dilated papilla at end of a long slender neck. Cyst covered with small papillae and indentations. Spores hat-shaped.

Genus 46. Sphaerocystis Labbé 1899:32. Epimerite a small sphere or ellipsoidal body at end of a long slender neck.

Genus 47. Lophocephalus Labbé 1899:31. Epimerite a large sessile flattened crateriform disc, the periphery crenulate and set at base with numerous short upwardly directed digitiform processes. Spores hat-shaped, black.

Genus 48. Cystocephalus Schneider 1886:99. Epimerite a large lance-shaped papilla set on a short stout cylindrical collar. Spores irregularly shaped.

Family 8. Stenophoridae Léger and Duboscq 1904:361. Development intercellular. Sporonts solitary. Epimerite absent or a simple structure. Cysts dehisce by simple rupture. Spores ovoidal with equatorial line. Not extruded in chains.

Genus 49. Oocephalus Schneider 1886:101. Epimerite a spherical button upon a short conical neck. Spores not known.

Genus 50. Stenophora Labbé 1899:15. Characters of the family. Confined to Diplopoda.

GENERA OF UNCERTAIN POSITION

Genus 51. Ulvina Mingazzini 1891:235.

Genus 52. Nematoides Mingazzini 1891:233. Dicystid, no septum in sporonts. Epimerite forked, situated on a long collar.

Genus 53. Ganymedes Huxley 1910:155. Associative, epimerite not known. Complete fusion of two individuals into one cytoplasmic mass. Cup at posterior end to aid in attachment. Spores unknown. Liver of crustaceans.

Genus 54. Agrippina Strickland 1912:108. Sporonts solitary, epimerite a circular disc armed with digitiform processes on periphery, short neck. Spores ellipsoidal.

POLYCYSTID GREGARINES IN THE DIPLOPODA*

NAME OF PARASITE	NAME OF HOST
Stenophora larvata (Leidy) Ellis	*Spirobolus spinigerus* Wood
Stenophora polydesmi (Lankester) Watson	*Fontaria virginensis* (Drury)
Stenophora julipusilli (Labbé) Crawley	*Julus* and *Parajulus*
Stenophora juli (Frantzius) Labbé	*Julus sabulosus* (L.)
	Julus boleti C. Koch
Stenophora dauphinia Watson	*Julus mediterraneus* Latzel
	Julus boleti C. Koch
	Julus fallax Meinert
Stenophora spiroboli Crawley	*Spirobolus* sp.
Stenophora fontaria (Crawley) Watson	*Fontaria* sp.
	Polydesmus sp.
Stenophora brölemanni Léger and Duboscq	*Blaniulus hirsutus* Bröl.
	Brachydesmus superus Latzel
	Brachyiulus pusillus lusitanus Verh.
Stenophora nematoides Léger and Duboscq	*Strongylosoma italicum* Latz.
Stenophora varians Léger and Duboscq	*Schizophyllum corsicum* Bröl.
Stenophora producta Léger and Duboscq	*Julus varius* Fabricus
Stenophora aculeata Léger and Duboscq	*Craspedosoma rawlinsii simile* Verh.
Stenophora polyxeni Léger and Duboscq	*Polyxenus lagurus* (L.) Lat.
Stenophora silene Léger and Duboscq	*Lysiopetalum foetidissimum* Savi
Stenophora chordeume Léger and Duboscq	*Chordeuma silvestre* C. Koch
Stenophora corsica Léger and Duboscq	*Craspedosoma légeri* Bröl.
Stenophora robusta Ellis	*Parajulus venustus* Wood
	Orthomorpha gracilis (C. Koch)
	Orthomorpha sp.

*The parasites are arranged in chronological order, under each genus.

Stenophora cockerellae Ellis	*Parajulus* sp.
Stenophora elongata Ellis	*Orthomorpha coarctata* (Sauss.)
Stenophora impressa Watson	*Parajulus impressus* (Say)
Stenophora lactaria Watson	*Callipus lactarius* (Say)
Stenophora diplocorpa Watson	*Euryurus erythropygus* (Brandt)
Cnemidospora lutea Schneider	*Glomeris* sp.
Amphoroides polydesmi (Léger) Labbé	*Polydesmus complanatus* (L.)
	Polydesmus dispar Silvestri
Amphoroides calverti (Crawley) Watson	*Callipus lactarius* (Say)

STENOPHORA LARVATA (Leidy) Ellis

[Figure 1]

1849	*Gregarina larvata*	Leidy	1849:232
1851	*Gregarina larvata*	Diesing	1851:553
1853	*Gregarina juli marginati*	Leidy	1853:237
1863	*Gregarina juli*	Lankester	1863:94
1875	*Stenocephalus juli*	Schneider	1875:584-5
1899	*Stenophora juli*	Labbé	1899:15
1903	*Stenophora juli*	Crawley	1903:51
1904	*Stenophora iulimarginati*	Léger and Duboscq	1904:362
1913	*Stenophora larvata*	Ellis	1913a:286

Stenophora: Sporonts solitary, elongate. Maximum length 800μ, maximum width 23μ. Ratio length protomerite : total length :: 1 : 20; width protomerite : width deutomerite :: 1 : 2. Protomerite small, subglobular, slightly flattened top and bottom, a flat circular papilla at apex with an apparent pore in center. A conspicuous constriction at septum. Deutomerite elongate-cylindrical, tapering gradually from center to an acute but bluntly pointed cone. Endocyte of protomerite clear, granular; of deutomerite dense and opaque. Nucleus small, spherical.

Taken at Philadelphia, Pa. Host: *Spirobolus spinigerus* Wood (*Julus marginatus* Say). Habitat: Intestine.

This species was observed by Leidy in 1849 and was the first gregarine he observed. His general statement regarding the parasite is quoted here nearly in full on account of its quaintness.

"Gregarina is probably the larva condition of some more perfect animal, but in the 116 individuals of Julus which I have examined, I have not been able to detect any form which could be derivable from it. Creplin doubts its animality. . . . I detected movements of an animal character, and this led me to seek for muscular structure, which resulted in the discovery of the longitudinal lines of the inferior cell. These escaped the observation of Siebold . . . In the state in which Gregarina is found, it would probably hold a rank between the Trematoda and Trichina, the lowest of the Nematoidea."

To Leidy, then, must be attributed the discovery of the longitudinal

striations in the epicyte and it is interesting to note that he discovered them during his first observations on the gregarines.

Leidy renamed the species four years later from the host in which it was found.

Lankester (1863:94), in a classification of the gregarines, grouped three of Leidy's forms: *G. larvata, G. juli marginati,* and *G. juli pusilli,* together with *Gregarina juli* Frantz. under the name of the latter, apparently because they were all parasites and the only known parasites of the same diplopod.

Schneider (1875:585) disregarding the rule of priority united *Gregarina juli marginati* and a species which he discovered under the name *Stenocephalus juli* (Leidy). His remarks are as follows:

"Cette espèce est commune et me parâit être identique à celle décrite par Leidy sous le nom de *Gregarina juli marginati.* Dans ce cas elle serait probablement répandue chez les différentes espèces du genre Julus, puisqui'on la connâitrait déjà chez trois d'entre elles. . . . L'espèce est légèrment polymorphe elle est tantôt très-allongée et relativement étroite, tantôt remarquablement massive; mais son protomérite demeure toujours identique à lui-même et suffit amplement au diagnostic."

Leidy gave no measurements of his species and Schneider based the identity of the two forms on the similarity of Leidy's figures with his material . It is true that in general shape the two are very similar but the protomerites differ slightly and the color differs markedly. Leidy's species is white; Schneider's yellow to yellow-orange. Because of these dissimilarities, the two forms should be separated.

Labbé (1899:15) changed the name of the genus *Stenocephalus* of Schneider to *Stenophora.*

Crawley (1903a; 634) did not consider the two species identical. His words are as follows:

"There is a good deal of confusion regarding the gregarines occurring in the Diplopod family Julidae. These gregarines all bear a certain amount of resemblance to one another, and it has been usual to relegate all of them to the species *Stenophora juli* Frantz. Léger and Duboscq (1903) have recently shown that such a procedure is not warranted for the fauna of Corsica and the case is certainly the same for that of the eastern United States. The Julidae of this region are infected with certainly two and possibly three species of Stenophora, while the classic *S. juli* apparently does not occur."

Léger and Duboscq (1904:361-2) take up the same discussion in their history of the Stenophoridae as follows:

"Leidy fit connâitre une Grégarine assez particulière, parasite de l'intestin de *Iulus marginatus* Say. Il l'appela d'abord (1851) *Gregarina larvata,* puis changea son nom en celui de *Gregarina iuli marginati* dans un travail postérieur (1853) ou il décrit une autre Grégarine, *G. iuli pusilli,* parasite d'un petit iule . . . qui n'est pas *Iulus pusillus* Leach.

Ray Lankester (1863) réunit les deux Grégarines de Leidy au *Stenophora iuli* de Frantzius, et cette synonymie fut admise par tous les auteurs qui suivirent.

Schneider (1875) le premier, décrivit avec précision la Grégarine parasite des *Iulus sabulosus* et *Iulus terrestris*. Il nota l'absence d'épimérite, la striation de l'épicyte trés marquée sur les 2 segments, la coloration jaune ou orangée de l'entocyte et le caractère des spores. Ces particularités lui firent crèer le genre Stenocephalus pour cette Grégarine qu'il identifia à la Grégarine décrite par Leidy dans *Spirobolus marginatus* Say. Il l'appela *Stenocephalus iuli* Leidy, nonobstant les règles de la nomenclature.

Stenocephalus iuli devint ainsi la seule Grégarine des Iules et Gabriel (1880) y rapporta de lui-même sa *Gregarina paradoxa*.

Dans les Sporozoa du Tierreich (1899) Labbé consacra les habitudes prises en ne reconnaissant pour Grégarine parasite des Iules que le *Stenophora iuli*. Il se contenda de remplacer le nom générique de Schneider par celui de Stenophora, le nom de Stenocephalus ayant été attribué antérieurement à un genre d'Hémiptères.

Howard Crawley (1903) étudiant les Grégarines des Iules et Paraiulus des Etats-Unis, rapporta les diverses espèces de Leidy au *Stenophora iuli*, tout en créant une nouvelle espèce pour un Stenophora d'un Spirobolus. Mais, dans un travail sue la faune de Corse (1903) nous avons montré que les Stenophora étaient representés par plusieurs espèces reconnaissables à la seule vue de céphalin. Notre facon de voir est adoptée par Crawley dans un second travail (1903a) et il restaure le *Stenophora iulipusilli* Leidy en soutenant que que le classique *Stenophora iuli* n'existe pas en Amerique.

Les espèces américaines de Stenophora se trouvent ainsi bien séparées du *Stenophora iuli* (Frantzius) Schneider. Nous (1903a) en avons détaché également un certain nombre de Stenophora des Diplopodes de Corse ou de Provence."

Stenophora larvata has not been found since Leidy's discovery of the species and its validity must be questioned until his work is substantiated by rediscovery of this parasite.

STENOPHORA POLYDESMI (Lankester) Watson

[Figures 2, 3, 4]

1853	*Gregarina polydesmi virginiensis*	Leidy	1853:238
1863	*Gregarina polydesmi*	Lankester	1863:94
1899	*Amphoroides polydesmi*	Labbe	1899:20
1903	*Gregarina polydesmivirginiensis*	Crawley	1903:45-46
1913	*Amphoroides polydesmivirginiensis*	Ellis	1913b:274
1916	*Stenophora polydesmi*	Watson	(This paper)

Stenophora: Sporonts solitary, elongate. Length 400-900μ*; width of deutomerite through widest part 25 to 60μ. Ratio length protomerite : total length :: 1:: 15 to 1 : 17; width protomerite : width deutomerite :: 1: 1.5 to 1 : 2 in normally extended individuals. Pro-

*Crawley (1903:46) gives 400μ as a maximum while Leidy gives 900μ.

tomerite subglobular to elongate, length twice the width. Slight constriction, if any, at septum. Protomerite as wide or wider than deutomerite at the septum. Deutomerite cylindrical, well rounded at posterior end. Endocyte tranluscent. Nucleus visible in vivo, ellipsoidal, one spherical karyosome.

Cyst and spores unknown.

Taken at Philadelphia and Wyncote, Pa., and Raleigh, N. C. Host: *Fontaria virginiensis* (Drury) *(Polydesmus virginiensis)*. Habitat: Intestine.

This species was described by Leidy (1863:238).

Léger (1892:132) described a species, *Amphorella polydesmi,* from the intestine of *Polydesmus complanatus* (L.). He created for the species a new genus, characterized by the presence of a short circular cup-like protomerite.

Labbé (1899:20) united the *A. polydesmi* of Léger and *G. polydesmi virginiensis* of Leidy as one species and because Amphorella was invalid, called the genus Amphoroides and the species *Amphoroides polydesmi* (Léger).

But the protomerite of *G. polydesmi virginiensis* does not coincide in shape with that of the genus Amphoroides, for it is subglobose and bears no indication of a cup-like depression which is characteristic of the latter genus; therefore it must be placed elsewhere. The three following factors coincide with those of the genus Stenophora, viz: a) subglobose protomerite, b) relative length of protomerite as compared with total length, c) solitary sporonts. The spores and the epimerite still remain undiscovered and until they are found the generic determination is, of course, not absolute.

Crawley (1903:45-6) called the species *G. polydesmivirginiensis* (Leidy), but in a later paper (1903a:640) he included it in a group of doubtful forms, all of which, however, he placed in the genus Gregarina.

Ellis (1913b:274) erroneously attributes to Crawley the assignment of the species name *Amphoroides polydesmivirginiensis.* It is Ellis himself at this point who names the species *A. polydesmivirginiensis* (Leidy). He offers no explanation therefor.

For the reasons given above, the species is now removed from the genus Amphoroides and placed in the genus Stenophora, the name now standing *Stenophora polydesmi* (Lankester) Watson. The trinomial of Leidy was shortened to a binomial by Lankester and this binominal must stand.

This is a well defined species, having been found and drawn by Crawley in 1903 and taken from the host in which it was originally found. The writer has examined a half dozen specimens of this diplopod taken at Urbana, without finding an instance of infection.

STENOPHORA JULIPUSILLI (Labbé) Crawley

[Figure 6]

1853	*Gregarina juli pusilli*	Leidy	1853:238
1863	*Gregarina juli*	Lankester	1863:94
1899	*Gregarina julipusilli*	Labbé	1899:35
1903	*Stenophora julipusilli*	Crawley	1903a:634-5
1904	*Stenophora iulipusilli*	Léger and Duboscq	1904:362

Stenophora: Sporonts solitary, elongate, rather stout. Maximum length 400μ, maximum width not given. Ratio length protomerite : total length :: 1 : 9 in adults; ratio width protomerite : width deutomerite :: 1 : 1.5. Shape protomerite conical with a rather sharp apex, widest below median portion, papilla with an apparent pore at anterior end, deep constriction at septum. Slightly broader than high. Deutomerite irregularly cylindrical, four times as long as broad, sometimes widest through middle, sometimes posterior to middle. Endocyte very dense in adults. Granules of protomerite different from those of protomerite. Nucleus spherical and large, attaining half the width of deutomerite. Contains a large karyosome. Cyst and spores unknown.

Taken at Philadelphia, Pa. Hosts *Julus* sp. and *Parajulus* sp. Habitat: Intestine.

This parasite was found and described by Leidy as *Gregarina julipusilli*. Both figures he gives appear to be those of immature specimens (see Fig. 5). From Leidy's data alone, I should consider the species invalid.

Crawley (1903:51) includes both *G. juli pusilli* and *G. juli marginati* with the classic *Stenophora juli* Frantzius under the name of the latter. That this determination was erroneous Crawley later discovered and (1903a:634-5) he separated the three species:

"This species is easily separated from *S. juli* by the size of the protomerite. In *S. juli* the length of the protomerite, according to the figures given by Schneider (1875) makes up only about 6% of the total length. In *S. julipusilli* this proportion increases to 10% in the adults and 15% in the young."

Stenophora julimarginati therefore stands as a separate, well defined species; the species described as *Gregarina juli pusilli* Leidy was renamed by Crawley as *Stenophora julipusilli* (Leidy). Crawley's words concerning the confusion of names are as follows:

"There is a good deal of confusion regarding the gregarines occurring in the Diplopod family Julidae. These gregarines all bear a certain amount of

resemblance to one another, and it has been usual to relegate them all to the species *Stenophora juli* Frantzius. . . . The Julidae of this region are infected with certainly two and possibly three species of Stenophora, while the classic *S. juli* apparently does not occur. Of these species, one is unquestionably the form described by Leidy (1853) as *Gregarina julipusilli.* As indicated by the specific name, Leidy considered its host to be *Julus pusillus* Say. According to Bollman (1887) this milliped, correctly *Julus minutus* Brandt does not occur in Pennsylvania, and it may be that Leidy was mistaken in his identification. This matter is not, however, of any great importance, and the specific name of the gregarine must stand. Leidy spelled the specific name of the host *pusullus,* whereas Say's memoir (1821) renders it *pusillus,* which spelling will be used for the name of the gregarine."

Leidy's original spelling of the host name (1853:238) *pusillus* is the correct one and the last remark of Crawley is uncalled for. The correct name of the diplopod, according to Bollman (1893), is now *Nemasoma minutum* (Brandt).

Since Leidy's description and figures are so inadequate and even his determination of the host possibly in error, there was no valid reason for Crawley's having retained the specific name *julipusilli* when he redescribed the species (1903a: 634-5).

Léger and Duboscq in the citation just given mention (1904) *S. iulipusilli* (Leidy) Crawley as a distinct species (note the last quotation).

In the specific diagnosis, given at the beginning of this species, Leidy's description was excluded. It is as follows:

"*Gregarina Juli pusilli.* White, translucent, oval. Cephalic sac hexahedral, with the sides rounded or forming a double cone, base to base, with the upper apex subacute or truncated in younger individuals. Posterior sac robust, oval; granular contents, fine, translucent; interior corpuscle, globular, transparent; nucleus transparent, without nucleolus. Whole length from 1 1500 in. to 1 275 in. Breadth of largest 1 500 in. Diameter of head of largest 1 1500 in. Hab. Intestine *Julus pusillus.*"

The name of this species must be a binominal and since Labbé was the first to give such a name to the particular species here designated, the species name becomes *Stenophora julipusilli* (Labbé) Crawley.

STENOPHORA JULI (Frantzius) Labbé

[Figures 7 and 8]

1848	*Sporadina Juli*	Frantzius	1848:195
1851	*Gregarina juli*	Diesing	1851:15
1863	*Gregarina juli*	Lankester	1863:94
1875	*Stenocephalus juli*	Schneider	1875:584-5
1880	*Gregarina paradoxa*	Gabriel	1880:371
1899	*Stenophora juli*	Labbé	1899:15
1903	*Stenophora juli*	Crawley	1903:51
1904	*Stenophora iuli*	Léger and Duboscq	1904:363-8

Stenophora: Sporonts solitary, elongate. Dimensions not given. Ratio length protomerite : total length :: 1 : 20 (approximately); ratio width protomerite : width deutomerite :: 1 : 2. Protomerite small, cylindrical at base, sharply conical above, little wider than high, a small papilla with an apparent pore at apex. Deutomerite elongate, slightly wider in anterior third than elsewhere, tapering gradually to an acute but blunt cone. Endocyte yellow to orange. Nucleus spherical, diameter half that of the deutomerite at its widest part, containing one large karyosome. Cysts dehisce by simple rupture. Spores fusiform with equatorial line.

Taken at Roscoff, France. Hosts: *Julus sabulosus* (L.); *Julus fallax* Meinert *(Julus terrestris)*. Habitat: Intestine.

Stenophora juli has been the source of more confusion and of greater discussion than any other gregarine parasitic in the diplopods. The too concise descriptions and the lack of any measurements of the animals by the earlier writers have led later workers to place a number of different parasites in this same group and to regard them all as *Stenophora juli.*

Frantzius' beautiful drawings are accompanied by no description beyond the statement that the parasite was found in Julus.

Diesing called the parasite *Gregarina juli* Frantzius. His description is as follows:

"Proboscis? Receptaculus capitellatum acutum brevissimum. Corpus longum fusiforme. Hab. *Julus terrestris* . . ."

Lankester (1863:94) relegated to this species the following: *Gregarina juli pusilli* Leidy, *G. juli marginati* Leidy, and *G. larvata* Leidy, all of which belong elsewhere, the last two being synonymous.

Schneider (1875:584-5) described a species as *Stenocephalus juli* from the intestine of *Julus sabulosus* and what he regarded as *Julus terrestris**. He considered his species as related if not synonymous with a species described by Leidy in 1853 as *Gregarina juli marginati.* His words are these:

"Cette espèce est commune et me parâit être identique à celle décrite par Leidy sous le nom de *Gregarina juli marginati.* Dans ce cas, elle serait probablement répandue chez les différentes espèces du genre Julus, puisqui'on la connâitrait déjà chez trois d'entre elles . . . L'espèce est légèrment polymorphe; elle est tantôt très-allongée et relativement étroite, tantôt remarquablement massive; mais son protomérite demeure toujours identique à lui-même et scuffit amplement au diagnostic."

Schneider overlooked the color factor in correlating the two species. Leidy described his *G. juli marginati* as "opaque, white." Schneider's *Stenocephalus juli* has the endocyte colored yellow or orange. Schneider gives no dimensions, but from the figure the proportions of his species agree perfectly with those of Leidy's species. The protomerites of the two species are slightly different in shape in the character of the papilla at the apex. The papilla in Leidy's species is large and flattened and the apparent pore is widest at the apex, narrowing as it approaches the endocyte; in Schneider's figure the papilla is smaller, more conical, either sharp or blunt at the end, slender in the middle, broadening at the base next the endocyte.

While the two species are obviously closely related, I am of the opinion that they are not identical. Crawley (1903a:634) says "the classic *Stenophora juli* apparently does not occur" in the United States and to date, 1915, it has not been described from this country.

If Schneider had given a set of dimensions for his species, that were identical with those of Leidy, the personal equation might have been considered to such an extent as to eliminate the color consideration and the variation in the two protomerites.

Leidy's *Gregarina julu marginati* is thus seen to be distinct from Schneider's *S. juli* and stands today as *Stenophora larvata* (Leidy) Ellis.

In 1880, Gabriel (p. 371) mentioned a species which he calls *Gregarina paradoxa* and says it is identical with *G. juli* (Frantz.) Schn. Neither description nor drawings accompany this statement and the reason for giving the species a new name, if it be *S. juli,* is not apparent.

*Léger and Duboscq (1904:364) say that *J. fallax* Mein. (*J. albipes* C. Koch) is probably the *J. terrestris* of Schneider.

Labbé (1899:15) unites under the name *S. juli* (Frantz.) Schn. all of the following:

1848 *Gregarina juli* Frantzius
1875 *Stenocephalus juli* Schneider
1851 *Gregarina larvata* Leidy
1853 *Gregarina juli marginati* Leidy
1880 *Gregarina paradoxa* Gabriel

Why Labbé regards them all as synonymous, he does not state. They appear to be alike only in that they are all parasites of the same diplopod, Julus. With the exclusion of the last three*, the species stands as containing the original *G. juli* Frantz. and *Stenocephalus juli* Schn. The ratios obtained from figures given by Frantzius and Schneider are almost identical. Neither author gives any dimensions, so the animals may agree not at all in actual size. The character of the endoplasm, its granular content and color, may differ considerably.

Léger and Duboscq give a detailed account of the various species which have been confused in the literature. For the entire quotation, see under the heading *Stenophora larvata* (Leidy) Ellis.

From a lack of positive evidence to the contrary, the two species *Gregarina juli* Frantz. and *Stenocephalus juli* Schn. stand as a single species, now called *Stenophora juli* (Frantzius) Schneider.

Léger and Duboscq (1904:363-8) described a parasite as *Stenophora juli* and considered it synonymous with the *S. juli* above. The animal which they described differs greatly from the classic *S. juli* in shape of all its parts, in its proportions, the density of its endoplasm, and in the shape of its nucleus (!). A detailed consideration of these factors is taken up under *Stenophora dauphinia.*

STENOPHORA DAUPHINIA Watson

[Figure 9]

1904	*Stenophora juli*	Léger and Duboscq	1904:363-8
1916	*Stenophora dauphinia*	Watson	(This paper)

Stenophora: Sporonts solitary, elongate. Total length 250 to 300μ. Width 19μ. Ratio length protomerite : total length :: 1 :10; width protomerite :: 1 : 0.9. Protomerite dilated in posterior two-thirds, separated from anterior part by a deep circular constriction. Apex broadly conical, papillate anterior end, with an apparent pore. Deutomerite cylindrical, attaining ten times the length of the protomerite.

*The third and fourth are synonymous being now *S. larvata;* the fifth is synonymous with *S. juli.*

Width nearly the same throughout and ending in a blunt rounded posterior extremity. Endocyte not described. Nucleus ellipsoidal, 1.7 times as long as wide. Cysts spherical, 250μ in diameter. Spores regularly ovoidal, epispore present. Equatorial line on spores.

Taken at Turin, Italy, and in Dauphine, France. Hosts: *Julus mediterraneus* Latzel *(Schizophyllum mediterraneum* Latz.); *Julus boleti* C. Koch *(Julus londinensis* Mein.); *Julus fallax* Mein. *(Julus albipes* C. Koch).

The authors described a parasite found in the same host as that upon which Schneider based his observations in his discovery of *Gregarina juli* (Frantzius). The species named by Schneider as the host of his parasites was *Julus terrestris* (Linnaeus) Porat but Léger and Duboscq observed that this species does not occur in France (1904:363).

"Nous décrirons d'abord *Stenophora iuli* (Frantzius) Schneider, qui nous a fourni de bons documents pour l'étude du développement des Stenophorides, et dont il importe de préciser la diagnose. Nous entendons par *Stenophora iuli* (Frantz.) Schneider le parasite de *Schizophyllum sabulosum* L. qui correspond à la description de Schneider. Cet auteur trouvait aussi *Stenophora iuli* dans *Iulus terrestris,* mais *Iulus terrestris* L. n'est pas une détermination. Depuis un siècle, les anastomistes appellent de ce nom tous les Iules qui sont de coleur noire, et le véritable *Iulus terrestris* (Linné) Porat ne parait pas exister en France. . . Et en effet, nous voyons dans un certain nombre d'Iules, une Grégarine bien voisine du parasite de *Schizophyllum sabulosum* L. Citons notamment parmi les hôtes de *Stenophora iuli, Schizophyllum mediterraneum* Latz. de la Tourraine, *Iulus londinensis* Mein. de la Tourraine, *Iulus albipes* C. K. du Dauphiné."

These authors base their observations on the parasites found chiefly in *Julus albipes.* In *Julus sabulosus* the gregarine attains a length of 450μ; in *J. fallax* Mein. and *J. boleti* C. K. of 300μ. Besides the elongate form, they mention a globular form nearly as wide as long, and reaching 130μ in length. They do not illustrate this form. The elongate sporont, only, is figured. The authors do not describe the shape of the various parts and make no comparison of their form with the classic *S. juli,* basing their identification rather on a similarity of hosts than of parasites.

The data and figures given by Léger and Duboscq (1904) and by Schneider (1875) compare as follows:

	Schneider	Léger and Duboscq
Total length	.....	450 max.
Total width	.....	.....
Ratio l. prot : total l	1 : 20	1 : 10
Ratio w. prot : w. deut	1 : 2	1 : 0.9
Shape protomerite	Apex papillate, with pseudo-canal, lower part cylindrical, upper part broadly conical, no constriction in protomerite.	Apex papillate with pseudo-canal, lower part broader than upper and separated from above by a deep circular constriction. Deep constriction at septum.
Shape deutomerite	Irregularly cylindrical, tapering from anterior third to a sharp but rather broad cone. Twice as wide at shoulder as at protomerite.	Regularly cylindrical, of approximately same width throughout, tapering slightly at posterior tip. Slightly narrower than protomerite.
Nucleus	Spherical. One large karyosome.	Ellipsoidal (1 : 1.7) with one large karyosome.
Shading in figure	Protomerite Dark Deutomerite Dark	Very light Dark

The proportions of the body dimensions, the shape of the two protomerites, and the shape of the two nuclei indicate at a glance that more than one species is under consideration and the species described by Léger and Duboscq should be renamed. I therefore designate it *Stenophora dauphinia.*

STENOPHORA SPIROBOLI Crawley

[Figure 10]

1903	*Stenophora spiroboli*	Crawley	1903:51
1903	*Cnemidospora spiroboli*	Crawley	1903a:638
1913	*Stenophora spiroboli*	Ellis	1913b:286

Stenophora: Sporonts solitary, elongate. Maximum length 1000μ; width not given. Ratio length protomerite : total length :: 1 : 32; width protomerite : width deutomerite :: 1 : 1.5. Protomerite small, rounded at anterior end, one-third as high as wide. Septum concave upward, thus forming a protomerite in the shape of a double convex lens. No constriction at septum; perfectly smooth contour throughout, from

end to end. Deutomerite elongate cylindrical, broadest just below septum where it attains one and a fourth times the maximum width of the protomerite. Slighly wider in anterior third than elsewhere, tapering slightly and terminating bluntly. Endocyte opaque in both protomerite and deutomerite. Nucleus undescribed, not visible in vivo. Cysts spherical, 350 to 500μ in diameter with thick epicyst. Dehiscence by rupture, spores fusiform, 12.5 by 7.5μ.

Taken at Raleigh, N. C. Host *Spirobolus* sp. Habitat: Intestine (?).

Crawley first described this species as *Stenophora spiroboli,* transferring it later to the genus Cnemidospora when the cyst and spores had been examined, probably because of the character of the spore-integument. The genus Cnemidospora Schn. (1882:446-7) is diagnosed thus:

> Protomerite subglobular, divided into two parts, the upper greenish gray, the lower yellow to brown; deutomerite elongate, cylindrical, spores ellipsoidal (nearly spherical) with a thick integument. No spore ducts in cyst.

The species in question does not coincide with the characters of the genus Cnemidospora. Neither the coloration of the protomerite nor the shape of the spores fits the generic description.

Ellis has replaced the species in the originally assigned genus, where it undoubtedly belongs because of the form and coloration of the sporonts, the character of the cyst dehiscence, and the shape of the spores.

STENOPHORA FONTARIA (Crawley) Watson

[Figures 11 and 12]

1903	*Amphoroides fontariae*	Crawley	1913:53
1913	*Amphoroides fontariae*	Ellis	1913b:274
1916	*Stenophora fontaria*	Watson	(This paper)

Stenophora: Sporonts solitary, ovoidal. Maximum length 135μ; width not given. Ratio length protomerite : total length :: 1 :4 to 1 : 5.5; width protomerite : width deutomerite :: 1: 1.5 to 1 : 2. Protomerite subglobose, widest in posterior two thirds, tapering to a blunt cone. Deep constriction at septum. Deutomerite elongate ovoidal, terminating bluntly. Endocyte nearly transparent in protomerite, very opaque in deutomerite. Nucleus not always visible in vivo, small, spherical, with one karyosome. Cyst and spores unknown.

Taken at Wyncote, Pa., Raleigh, N. C., and at East Falls Church, Va. Hosts: *Polydesmus* sp. and *Fontaria* sp. Habitat: Intestine.

Léger (1892) created the genus Amphorella, afterwards renamed Amphoroides by Labbé (1899:20), to include species with solitary ovoidal sporonts having a protomerite short, compressed and crateriform, and

spores rhombus-shaped (seen in one plane) and biconical, with but one integument.

Léger and Duboscq (1904:375) compared one of their new species with the species in question. Their remarks are:

"*Stenophora chordeume* nous paràit, par sa forme, une espèce très voisine de la Grégarine des Polydesmus et Fontaria des Etats-Unis, signalée par Crawley (1903) sous le nom d' *Amphoroides fontariae*. Les figures qu'en donne cet auteur dans sa Pl. I fig. 12, 13, 14 nous portent à croire, d'après les caractères de l'épimérite, qu'il s'agit plutôt d'un Stenophora que d'un Amphoroides. Il est d'ailleurs impossible de se prononcer avec certitude sur ce point, car Crawley ne nous fait pas connaitre les sporocystes de sa Grégarine, et on sait que, outre la forme de l'épimérite, celle des sporocystes distingue nettement les Amphoroides des Stenophora; dans Amphoroides, ils sont biconiques; chez Stenophora, ils sont ovoides."

Thus the basis for the original inclusion of the species in the genus Amphoroides is not that of spore characteristics and until the spores are known the generic position of the species will not be absolute. The shape of the protomerite of the species under consideration is, however, very unlike that of the type species of this genus, *A. polydesmi* Léger, and hence the species cannot consistently be left in this genus. Its logical position seems to be with the Stenophoridae because of elimination from any other genus rather than from any positive character, and I should designate it *Stenophora fontaria* (Crawley).

STENOPHORA BRÖLEMANNI Léger and Duboscq

[Figure 13]

1903 *Stenophora brölemanni* Léger and Duboscq 1903a:339-40

Stenophora: This gregarine is small, from 40 to 54μ long and is compressed laterally, especially in the anterior part. It lives within the cell of the host during the greater part of its life cycle. The older intercellular individuals are subspherical and occupy a cavity larger than that occupied by the younger ones, which is formed by the greater destruction and compression of surrounding cells. The protomerite is invaginated into the anterior end of the deutomerite like a cork into the neck of a bottle. When the animal leaves the epithelium, the protomerite still retains its invaginated position. The protomerite in profile is cylindrical, rather flattened at the top, and when seen from the front it is as broad as high, widest anterior to the middle and possesses at the summit a small plate slightly concave upward and bearing in the center a small spherical papilla. Léger and Duboscq say this papilla may correspond to a protractile epimerite, for fibrillae seem to radiate from the apex outward over the anterior third of the protomerite. The deutomerite seen in profile is much larger at its posterior end than elsewhere, i. e., the animal is com-

pressed chiefly in the anterior half. A front view shows a deutomerite as broad as it is high. The nucleus is large, spherical or slightly ovoidal and contains one large karyosome. The parasite is characterized then by its compression, the invagination of its protomerite and by its inter- or intra-cellular location (the authors are not sure which).

Taken in Provence, France, and on the island of Corsica. Hosts: *Blaniulus hirsutus* Bröl., *Brachyiulus superus* Latzel, *Brachyiulus pusillus lusitanus* Verh. Habitat: Intestine.

STENOPHORA NEMATOIDES Léger and Duboscq

[Figures 14 and 15]

1903 *Stenophora nematoides* Léger and Duboscq 1903a:335-7

Stenophora: Sporonts solitary, elongate. Average length 170μ, maximum length 300μ. Width not given. Ratio length protomerite : total length :: 1 : 10; width protomerite : width deutomerite :: 1 : 3. Protomerite cylindrical, slighly dilated a little anterior to septum. Twice as long as wide, dome shaped at apex; constriction at septum. Deutomerite normally with constriction at end of anterior third, or half; above this point considerably dilated, especially in posterior portion. Posterior half or two thirds of deutomerite, i. e., part below constriction, cylindrical, ending in a broadly rounded or somewhat truncate extremity. The largest sporonts without the peculiar dilated portion of the deutomerite; nematoid in shape, long, slender, cylindrical, often slightly curved and with a body as much as seventeen times as long as to protomerite (170 : 10), and not more than 7μ wide throughout. Endocyte granules fine, homogeneous except in anterior end of protomerite where deeply staining chromatic granules are accumulated. Nucleus large and ovoidal, the long axis parallel to the long axis of the body. One large karyosome. Epimerite a large subglobular hyaline body. Cyst and spores unknown.

Taken at Bastia, Corsica. Host: *Strongylosomum italicum* Latzel. Habitat: Intestine.

The authors' conclusion concerning this species is as follows:

"Bien que nous ne connaissions pas l'évolution complète de cette Grégarine, nous avons la conviction qu'il s'agit d'une espèce voisine du *Stenophora iuli*, car à part la forme générale nématoide qui est ici très caractèristique de l'espèce, toutes le autres particularitiés structurales (forme du protomérite, caractère du noyeau, présence de grains chromatoides accumulés surtout dans le protomérite, etc.) se retrouvent aussi chez les autres espèces du genre Stenophora, lequel d'ailleurs est spécial aux Diplopodes."

STENOPHORA VARIANS Léger and Duboscq

[Figures 16 and 17]

1903 *Stenophora varians* Léger and Duboscq 1903a:337-9

Stenophora: Sporonts solitary, dimorphic, elongate and globular. The elongate forms cylindrical or slightly compressed, slightly attenuate at both extremities, attaining a maximum length of 250μ. Width not stated. Ratio length protomerite : total length :: 1 : 6 to 1 : 7; ratio width protomerite : width deutomerite :: 1 : 1. Protomerite cylindro-conical, 1½ times as long as wide, its summit depressed, with an apparent pore. Constriction at septum. Deutomerite just below septum a little narrower than protomerite a short distance above. Deutomerite irregularly cylindrical, slightly curved in adults, truncate or broadly rounded behind. Nucleus spherical with a large karyosome. Endocyte of protomerite consisting of large deeply staining bodies, of deutomerite large non-staining bodies with a few scattered chromatic bodies.

The globular sporonts more rare than the elongate ones but coexisting with the latter. Maximum length 35 to 40μ. Deutomerite large, globular protomerite, cylindro-conical and shorter than in the elongate forms. A small papilla at anterior end. Protomerite shows same staining reaction as elongate forms and the nucleus is relatively larger, with a much larger karyosome.

Taken at Ajaccio, Corsica. Host: *Schizophyllum corsicum* Bröl. Habitat: Intestine.

Relative to the dimorphism, the authors make these remarks:

"Au sujet de interprétation de ces deux formes de Stenophora dans un même hôte, on peut émettre plusieurs hypothèses: On bien la forme globuleuse, on raison de sa petite taille représente un stade très jeune de la Grégarine; ou elle représente une espèce distincte de la forme allongée; ou bien enfin il s'agit d'un dimorphisme sexuel dans des individus d'une seule et même espèce. Nous nous rattachons d'autant plus volontiers à cette dernière hypothèse que l'on observe assez souvent de jeunes formes allongées de volume bien inférieur à celui des formes globuleuses."

The great difference in maximum lengths recorded of the elongate (250μ) and the globular (40μ) forms of this species would hardly indicate that the latter is mature. The immature specimens of most species of gregarines are more or less globular, stain deeper, have a protomerite which changes but little in shape as maturity approaches, and possess nuclei much larger in proportion than the adults, and often of a different shape from that of the adults. I have often seen these globular individuals as large or a little larger than other individuals which had al-

ready assumed their adult form, and have attributed the difference to a difference merely in the amount of nourishment they have received. I think if we are to assume that there is a sexual dimorphism, we must look for two individuals of somewhere nearly the same size rather than one six times the size of the other.

While sexual dimorphism is a factor to be looked for among gregarines, it has never been definitely proven for a single species. There may be a difference in sexes among the sporonts, but if so, this difference seems to be of a chemical nature or of such slight morphological significance as to have been generally overlooked; and it should be evident among all or most of the members of the same family rather than confined to a few species only.

STENOPHORA PRODUCTA Léger and Duboscq

[Figure 18]

1903	*Stenophora iuli*	Léger and Duboscq 1903a:315
1904	*Stenophora producta*	Léger and Duboscq 1904:375-7

Stenophora: Sporonts solitary, very elongate. Sporonts 1000μ long, width not given. Ratio length protomerite : total length :: 1 : 20; ratio width protermite : width deutomerite :: 1 : 21. Protomerite globular, slightly flattened top and bottom, sometimes slightly invaginated at the deutomerite. At apex a small papilla with an apparent pore. Deutomerite very long, cylindrical, broadly rounded behind. Endocyte of protomerite finely granular, staining deeper than the deutomerite. The nucleus ellipsoidal, with one large karyosome. An inverted xiphoid cone rounded at the summit, projecting from the septum downward into the deutomerite and consisting of homogeneous protoplasm staining deeper than that of the deutomerite. Probably consisting of nutriment manufactured by the protomerite and filtered through the septum, to be eventually diffused through the deutomerite. Epimerite a small knob. Cysts spherical, size not given. Spores ovoidal, 5μ long.

Taken at Corte, Corsica. Host: *Julus varius* Fabricus *(Parajulus varius* Fab.). Habitat: Intestine.

The reason for the confusion of names mentioned above appears in the following quotation from Léger and Duboscq (1904:375):

"Nous avons déjà signalé la présence de cette Grégarine dans l'intestin de *Pachyiulus varius* Fab. de la Corse (1903) et nous l'avons tout d'abord confondue avec *Stenophora iuli,* ne l'ayant observée a cette époque que sûr le vivant. Depuis une étude plus approfondie sur des préparations colorées nous a convaincu qu'il s'agit d'une espècee morphologiquement différente de *Stenophora iuli* (Frantzius)

Schneider et nous la distinguerons de cette dernière sous le nom de *Stenophora producta* n. sp. . . . Nous n'avons pas remarqué de ligne équatoriale à la surface des sporocystes de *Stenophora producta,* ce qui distingue encore cette espèce de *Stenophora iuli.*"

STENOPHORA ACULEATA Léger and Duboscq

[Figures 19 and 20]

1904 *Stenophora aculeata* Léger and Duboscq 1904:368-70

Stenophora: Sporonts solitary, elongate. Maximum length 60μ; width not given. Ratio length protomerite : total length :: 1 : 4 (approx.); width protomerite : width deutomerite :: 1 : 15. Protomerite subglobular, a short cylindrical portion at the base, somewhat dilated in middle, terminating in a small delicate elongate papilla 1 to 2μ long. A conspicuous constriction at septum. Deutomerite cylindrical, broadly rounded behind. The endocyte of the deutomerite with protoplasmic granules smaller than those of protomerite and less deeply staining. Nucleus very large, subspherical in diameter, two thirds to seven eights the width of deutomerite, with a large karyosome. Cysts and spores unknown.

Taken in Dauphine, France. Host: *Craspedosoma rawlinsii simile* Verh. Habitat: Intestine.

STENOPHORA POLYXENI Léger and Duboscq

[Figure 21]

1900 *Stenophora polyxeni* Léger and Duboscq 1900:1566-8
1903 *Stenophora polyxeni* Léger and Duboscq 1903:xciii
1904 *Stenophora polyxeni* Léger and Duboscq 1904:370-1

Stenophora: Sporonts solitary, obese. Average length 80μ. Width not given. Ratio length protomerite : total length :: 1 : 10; ratio width protomerite : width deutomerite :: 1 : 2 (approx). Protomerite very small, hemispherical or somewhat flattened. No apparent pore in anterior end, as in many Stenophoridae. Protomerite twice as wide as high. Widest at or just above base. Slight constriction at septum. Deutomerite elongate ovoidal in young and sac-shaped in older sporonts. Endocyte fairly homogeneous. Nucleus spherical, half the width of deutomeritet, with a large karyosome. Cyst and spores not known.

Taken at Grenoble, France. Host: *Polyxenus lagurus* (Linn.) Latreille. Habitat: Intestine.

STENOPHORA SILENE Léger and Duboscq

[Figures 22 and 23]

1904 *Stenophora silene* Léger and Duboscq 1904:371-2

Stenophora: Sporonts solitary, dimorphic, an elongate and a globular form. The elongate form 100μ in maximum length, width not given. Ratio length protomerite : total length :: : 1 : 10; width protomerite : width deutomerite :: 1 : 1. Protomerite cylindrical, slightly dilated top and bottom, nearly flattened at top, an apparent pore at apex. Constriction at septum. Deutomerite cylindrical, gradually tapering toward posterior end. Endocyte of protomerite with large achromatic bodies, of deutomerite very finely granular and deeply staining. Nucleus large, half the maximum width of deutomerite, ovoidal, its longitudinal axis parallel to that of body, containing one large karyosome.

The globose form, 55 to 60μ in maximum length. Width not given. Ratio length protomerite : total length :: 1 : 6; width protomerite : width deutomerite :: 1 : 2.3. Protomerite similar to that of elongate form, but containing finely granular endoplasm as deeply staining as that of deutomerite. Deutomerite broadly ovoidal, widest below center. Nucleus less ellipsoidal than in elongate form. Cyst and sports not known.

Taken in Dauphine, France. Host: *Lysiopetalum foetidissimum* Savi. Habitat: Intestine.

"Howard Crawley (1903) a signalé dans *Lysiopetalum lactarium* des Etas-Unis deux espèces de Grégarines: l'une qu'il nomme *Gregarina calverti* dont la forme générale et la taille sont si differentes de celles de la précédente que l'on ne peut établir de confusion; l'autre espèce est rapportée au *Stenophora iuli.* Il est possible que celle-ci soit identique à notre *Stenophora silene,* mais on ne peut l'affirmer, car Crawley ne donne pas de dimensions de son Stenophora."

Stenophora silene is not the species described by Crawley (1903:51; 1903a:634-5) as *Stenophora juli.* Crawley's species attains a length of 400μ, *S. silene* of only 100μ. The protomerite of *S. juli* is broadly conical, 1.4 times as wide as high; of *S. silene* cylindrical, flattened at the apical end. Crawley's *Gregarina calverti* is still another species, now called *Amphoroides calverti.*

Whether or not there is an actual dimorphism in the Stenophoridae is a problem still far from settled. The finding of elongate and globose forms in the same species and the difference in staining reactions can, I think, hardly be considered sexual dimorphism unless the two sporonts are of somewhere nearly the same size. In *S. silene,* the difference in length of the two is 100%. The difference in lengths of the elongate

and globular sporonts is not to be accounted for by a mere shortening of the body, for the staining reaction and shape of the nucleus differ as well. The nucleus of the globular form is less ellipsoidal than that of the elongate form. In all Stenophoridae I have observed, the young trophozoites and younger sporonts have not yet attained that elongation of the nucleus which is characteristic of the adults, and a gradual transition can be observed in the same series of sections from a spherical to sub-spherical and finally to the elongate ellipsoidal nucleus of the adult. In all the gregarines I have studied, the young globular trophozoites contain less protoplasm and stain more readily and deeper than the adults.

If globular and elongate specimens of approximately the same length can be procured or, at least, with protomerites of the same approximate size, and a young cyst shown to contain two individuals with different staining rections and differently shaped nuclei, then there is sexual dimorphism among the Stenophoridae. This has not yet been reported and there is too great a discrepancy in size of the elongate and globose forms to warrant calling them sexually unlike and the phenomenon sexual dimorphism.

STENOPHORA CHORDEUME Léger and Duboscq

[Figures 24 and 25]

1904 *Stenophora chordeume* Léger and Duboscq 1904:372-5

Stenophora: Two forms described for the sporonts. Elongate form 140μ long, width not given. Ratio length protomerite : total length :: 1 : 7.5; width protomerite : width deutomerite :: 1 : 2. Protomerite nearly twice as wide as high, widest along central portion, flattened above, with papilla and an apparent pore at apex. Conspicuous constriction at septum. Deutomerite an elongated irregularly shaped sac widest below the middle and tapering rapidly to a point. Endocyte of protomerite clear, containing large non-staining granules. Endocyte of deutomerite homogeneous with a few scattered irregularly shaped chromatic granules. Nucleus spherical, with a large karyosome.

Globular form with maximum length of 100μ. Width not given. Ratio length protomerite : total length :: 1 : 5; width protomerite : width deutomerite :: 1 : 2.5. Protomerite same shape as in elongate form except that the constriction at septum is deeper and the protomerite sometimes partially invaginated into anterior end of deutomerite. Latter ellipsoidal and nearly spherical. Endocyte of protomerite deeply staining, like that of deutomerite. Latter with long scattered chromatic

filaments. Nucleus spherical, with a large karyosome and numerous irregular chromatic granules. Cyst and spores unknown.

Taken at Grenoble, France. Host: *Chordeuma silvestre* C. Koch (*C. sylvestre* C. K.). Habitat: Intestine.

Concerning the long chromatic filaments in the deutomerite, the authors say (1904:374):

"Sur la signification de ces singulières formations, on ne peut qu'émettre des hypothèses: ou bien ce sont des productions parasitaires, ce qui nous paraît peu probable, car toutes les formes globueuses en montrent à l'exclusion des formes allongées, ou bien ce sont des produits dèrivés de l'activitié cellulaire. Tout en nous rattachant plus volontiers à cette manière de voir, nous ne saurions dire si ces produits prennent naissance dans le cytoplasme comme substances de réserve ou de déchet comparables aux cristalloides déjà signalés chez certaines Grégarines, ou bien s'ils dérivent de la chromatine nucléare. Dans tout les cas, nous ne croyons pas devoir les considérer comme des éléments chromatiques ou chromatides, destinés a jouer un rôle important dans les phénomènes sexuels et nous les regardons plutôt comme des produits ergastoplasmiques."

As heretofore, the size of the two dimorphants is considerable (50%). The deutomerite of the smaller contains many long chromatic filaments. At the same time, the deutomerite of the elongate form is not devoid of scattered chromatin, which may be the broken remnants of threads in a younger stage. Only two diplopods were parasitised, one harbored many parasites; the other on the contrary very few. It is possible, from the limited material at hand, that still longer and more mature elongate forms may exist and bring up the percentage still higher.

For the views of the authors concerning its relationships compare the paragraph quoted under *Stenophora fontaria* (page 60).

From the data given, then, it is impossible to state with certitude that the species are or are not the same. Dimensions correspond closely. I have not included Crawley's species here because of difference in shape of the sporonts but have left it as a distinct species and placed it among the Stenophoridae, the name now being *Stenophora fontaria* (Crawley).

STENOPHORA CORSICA Léger and Duboscq

1903 *Stenophora corsica* Léger and Duboscq 1903a:314

No description or figure is given for this species. It is merely mentioned as a parasite found in *Craspedosoma legeri* Bröl. at Vizzanova, on the island of Corsica.

STENOPHORA ROBUSTA Ellis

[Figure 26]

1912 *Stenophora robusta* Ellis 1912a:8-10

Stenophora: Sporonts solitary, relatively short and thick. Average length 153μ; minimum length 140μ; maximum 180μ. Width 67μ, as average. Ratio length protomerite : total length :: 1 : 8; with protomerite : width deutomerite :: 1 : 2.5. Protomerite small, dome-shaped or conical. Slight concavity in apical portion, widest at junction with deutomerite. No constriction at septum. Deutomerite broadly ellipsoidal, widest in center, slightly rounded behind. Endocyte fairly clear in all parts but especially so in protomerite. Nucleus spherical, faintly visible or obscured in vivo. One or more karyosomes. Cyst and spores not known.

Taken at Boulder, Colo. Hosts: *Parajulus venustus* Wood; *Orthomorpha gracilis* (Koch); *Orthomorpha sp.* Habitat: Intestine.

STENOPHORA COCKERELLAE Ellis

[Figure 27]

1912 *Stenophora cockerellae* Ellis 1912:681-5

Stenophora: Sporonts solitary, elongate. Average length 500 to 800μ. Minimum length 186μ; maximum 850μ. Width deutomerite not given. Ratio length protomerite : : ::1 : 14.5 to 1 : 17 in adults; width protomerite : width deutomerite :: 1 : 2. Protomerite more or less globose, widest in posterior half. Slightly constricted at septum. Peculiar in that the protomerite protrudes and retracts a short rounded papilla. Deutomerite widest in anterior sixth. Posterior end broadly rounded to square. Endocyte of protomerite pale gray, rather opaque, nearly filling protomerite. Endocyte of deutomerite dense, lead gray to almost black. Nucleus spherical, diameter two thirds the width of deutomerite. Not visible in vivo. Cyst and spores unknown.

Taken at Quirigua, Guatemala. Host: *Orthomorpha coarctata* Intestine.

STENOPHORA ELONGATA Ellis

[Figure 28]

1912 *Stenophora elongata* Ellis 1912:685-6

Stenophora: Sporonts solitary, very elongate. Length 200 to 300μ (average). Minimum length 21μ; minimum 390μ. Width of deutomerite not given. Length of protomerite : total length :: 1: 18 to 1 : 26; width protomerite : width deutomerite :: 1 : 1:6. Protomerite more or less pentagonal (seen from side), truncate, wider than long. Constriction at septum distinct. Deutomerite widest in anterior third, posterior end rounded. Endocyte of protomerite dense, opaque, dark gray; of deutomerite gray, very dense. Nucleus not visible in vivo, spherical, one half to seven eighths width of deutomerite. Cyst and spores unknown.

Taken at Quirigua, Guatemala. Host: *Orthomorpha coarctata* (Saussure). Habitat: Intestine.

STENOPHORA IMPRESSA Watson

[Figure 53]

1915 *Stenophora impressa* Watson 1915:29

This parasite was found to be very common in the intestine of *Parajulus impressus* (Say), one of the common small diplopods found at Urbana, Illinois.

The sporonts are isolated, none being associative. They are elongate ellipsoidal in shape, widest through the central portion of the deutomerite or at the beginning of the posterior two thirds. The protomerite is conical, dilated just above the base and tapering rather acutely but with a blunt point at the apex. The widest part is some little distance anterior to the septum, the constriction at the septum being conspicuous but not deep. The length of the protomerite is about one tenth of the total length of the sporont. The deutomerite broadens gradually from the septum to the central region and then as gradually becomes narrower, ending in a very blunt extremity of much the same general shape as the anterior end of the protemerite. At its widest part, the deutomerite is about twice the greatest width of the protomerite.

The endocyte is gray with no trace of tan. The protomerite contains a few large granules of more or less transparent protoplasm and the deutomerite content is finely granular, homogenous, and often so dense as to appear black in transmitted light. The epicyte is thin, transparent, of even width throughout, and is longitudinally striated. At the anterior end of the protomerite there is an invagination of the epi-

cyte. The latter is here very thin and readily breaks, with a consequent extrusion of the endocyte. The nucleus is spherical, generally visible in the adults and contains one large karyosome which is visible without staining.

The trophozoite of *Stenophora impressa* was studied in sections made of the intestine of the parasitised Parajuli. The young parasites lie imbedded between the cells of the intestinal epithelium, having made a place for themselves by the absorption and destruction of the cell originally entered, and by the absorption, destruction, and pushing aside of contiguous cells; they lie with the apex of the protomerite next the mesothelial wall. As is often the case with the Stenophoridae, there is never developed an epimerite. Since the whole parasite lies embedded, there is abundant surface through which osmosis may take place without the additional presence of an epimerite. The protomerite of trophozoites is often deeply embedded in the deutomerite, like a cork in the neck of a bottle.

Two types of movement were observed. A rapid gliding over the surface at the rate of 6μ per second was very common. This form of movement persists for an hour or more after the animals are placed on the slide. Partial rotation of the body on its own axis and a bending of the body to an angle of about 45° were frequent. The epicyte in the region just below the septum is very flexible, resulting in a nodding of the protomerite from side to side. The extension of the upper part of the deutomerite which causes the protomerite to drop is effected slowly, but withdrawal of protoplasm is done by a sudden jerking movement which restores the normal shape.

Cysts 160μ in diameter were found, but none could be induced to develop to completion in a water medium.

This species differs from *Stenophora lactaria* in a) general shape of the deutomerite, b) shape of the posterior end of the body, and c) shape of the nucleus.

A table of the various dimensions given in microns follows:

Total length of body	155	270	240	270	390	345
Length of protomerite	20	30	25	25	35	30
Length of deutomerite	135	240	215	245	355	315
Width of protomerite	30	35	35	30	48	48
Width of deutomerite	70	70	70	70	115	100
Ratio						
length protom.: total length	1:7.5	1:9	1:10	1:10	1:11	1:11
width protom.: width deutom.	1:2.3	1:2	1:2	1:2.3	1:2.4	1:2.1

STENOPHORA LACTARIA Watson

[Figure 55]

1915 *Stenophora lactaria* Watson 1915:29-30

A gregarine which was found with relative frequency is this one from the intestinal tract of the small diplopod *Callipus lactarius* (Say), taken at Urbana, Illinois, during the month of October, 1914. The infection per host was heavy and sections of the alimentary tract showed the latter half of the same to be heavily parasitised.

A table of various dimensions of the parasites at different ages follows. There is considerable discrepancy in the ratios given but the fact that there is a gradual transition from one extreme to the other indicates that a single species is involved. Measurements were made only of individuals which to all appearances were equally expanded; dimensions are all given in microns:

Total length sporont	175	216	293	304	339	455	480
Length protomerite	28	27	30	30	20	36	30
Length deutomerite	145	189	213	264	319	419	450
Width protomerite	30	30	39	29	39	35	39
Width deutomerite	54	53	90	61	90	65	90
Ratio							
length protom.: tl. length	1:6	1:7.5	1:10	1:10	1:17	1:13	1:16
width prot.: width deut.	1:1.8	1:1.8	1:2.3	1:2.1	1:2.3	1:1.9	1:2.3

The sporonts, as in all members of this family, are solitary until just previous to cyst formation. The body, when moderately expanded, is shaped like a classic vase, widest near the top and tapering very gradually. The protomerite is small in comparison with the deutomerite, being from one eighth (in young specimens) to one sixteenth the total length. It is conical, widest just anterior to the base, and its breadth exceeds its height. (39 by 30μ; 32 by 29μ). It is from 0.4 to 0.6 as wide as the deutomerite at its widest part. There is a slight invagination at the anterior end. The deutomerite is widest a short distance below the conscription at the septum and tapers gradually toward the posterior end, terminating in a blunt cone.

The protomerite is quite or nearly transparent, containing but few large crystal granules of protoplasm which stain deeply. There is an apparent pore at the anterior end. The deutomerite is more or less dense and opaque, being pearly white in reflected light and light or dark gray, depending on the amount of protoplasm present, in transmitted light. The density depends on age, the young trophozoites containing a few pale gray granules, the oldest and largest sporonts being filled with pro-

toplasm which gives to them a blackish appearance. The deutomerite stains a fairly homogeneous shade, and the small granules here do not absorb as much of the stain as do the larger protoplasmic granules.

The epicyte is colorless and very thin, even at the septum. Longitudinal striations are discernible. This epicyte is much more resistant than in many gregarines studied, for animals remain alive on the slide in a water medium or in normal saline for many hours, and when they finally become immotile, retain their shape. After several days on the slide, they have been noted to be intact with the body only a little more nearly globular from osmosis than in the normal parasites. This may be due to the thinness of the epicyte and its great permeability. Myonemes were seen in stained sectioned specimens as deeper staining dots, larger than the deutomerite granules and lying along the periphery of the endocyte in the longitudinal striations.

The nucleus of sporonts is an elongate ellipsoid, generally placed diagonally and reaching almost entirely across that part of the deutomerite in which it lies. In large specimens, it approximates 55 x 30μ. It contains one large spherical or slightly ovoidal karyosome which stains evenly and lightly throughout with Ehrlich's hematoxylin. The nucleus is not visible in vivo in the large and dense individuals. In young specimens, it is spherical, becoming ellipsoidal as the sporont stage approaches.

The trophozoite is much less dense than the sporont. The epimerite is a round, sessile, transparent knob.

The sporozoite is a deeply staining, spindle shaped body which penetrates the cell at is free end, becomes embedded, grows, and absorbs the host cell which it entered. The whole trophozoite, not merely the epimerite, lies embedded and after it has destroyed the originally entered cell distorts and compresses those adjoining. It remains embedded until it has practically outgrown the cells of the epithelium and easily escapes into the lumen through the canal it has formed by cell destruction. The trophozoite is able to move about while embedded. In cross sections of the intestine the parasite, still embedded, is sometimes cut crosswise, indicating that it lies with its longitudinal axis parallel to that of the host, and in one instance it lay with the protomerite pointed toward the lumen rather than toward the mesothelial wall, the normal position.

The gliding movement common to most Polycystids is functional here and the animal moves forward very rapidly in a straight line, often with a constant turning of the protomerite from side to side which affects neither the rapidity nor the direction of motion. Progression has been observed at the rates of 6.5μ and 7.5μ per second. Each of these rates is for a different specimen and each movement extends at a uniform rate over several minutes. No gelatinous stalk was seen trailing the ani-

mal either with or without the use of a stain on the slide. Ameboid movement was noted, chiefly confined to the anterior part of the deutomerite; it results in the nodding of the 'head' as many as thirty times without ceasing or decreasing speed. The protomerite does not change in shape or size, neither does the posterior two thirds of the deutomerite. The epicyte of the shoulder region stretches on one side, the endocyte flows into the pocket thus formed, and the inactive protomerite, its equilibrium disturbed, drops to one side and then to the other as the pockets form now on one side and now on the other. Structures which cause movement must therefore be much more numerous or else much more active physiologically in this restricted area than elsewhere.

Cysts are spherical and vary from 150 to 270μ in diameter. I have as yet been unable to procure development of the cysts. A number were kept from two days to two weeks in water and normal saline media and when opened revealed no indication of having undergone progression beyond the dissolution of the walls separating the two conjugants. Staining revealed no differentiation whatever in the apparently homogeneous protoplasm.

This species is distinguished from *Stenophora larvata* (Leidy) Ellis by the considerable difference in size. Leidy's species varies from 100μ to 800μ in length, while *S. lactaria* does not exceed 480μ. His form varies in width from 30μ to 20μ, the other never exceeding 90μ. The ratio of length protomerite : total length in *S. larvata* (largest individual) is 1 : 26; in *S. lactaria* it never exceeds 1 : 16. The nucleus in the former is spherical and about 70μ in diameter; in the latter it is ellipsoidal and smaller, 55 by 30μ in the largest measured. The host is a different diplopod found, however, in the same habitat.

S. lactaria differs from *S. elongata* Ellis and from *S. cockerellae* Ellis in size, shape of the protomerite and deutomerite, and in shape especially of the posterior end of the deutomerite.

STENOPHORA DIPLOCORPA Watson

[Figure 54]

1915 *Stenophora diplocorpa* Watson 1915:29

A number of most peculiar polycystid gregarines were found in the common small diplopod, *Euryurus erythropygus* (Brandt), at Urbana, Illinois. The parasites were abundant in each of the two specimens examined, each host containing more than a dozen gregarines.

The sporonts are solitary. The shape is more or less cylindrical, the body being very much attenuated. The protomerite is as wide as it is long and is from one-sixteenth to one-twenty-fifth the total length of the

body, and there is no indentation at its anterior end as in many of the Stenophoridae. The anterior half of the protomerite is rather broadly conical and is blunt at the apex. There is but a slight constriction at the septum in extended individuals. The anterior end of the deutomerite is but little wider than the protomerite just in front of the septum. The deutomerite gradualy widens, becoming twice the maximum width of the protomerite. It is incompletely separated into two nearly equal parts by a deep constriction at about the middle and behind this constriction the body is cylindrical, of practically the same width throughout, terminating in a blunt, well rounded cone.

The protomerite is transparent or nearly so, containing a few large irregular deeply staining granules clustered near the septum. The deutomerite is plain tan in color and contains smaller homogeneous granules densest just anterior to the constriction in the walls, least dense at the posterior end, and otherwise fairly evenly distributed. The endoplasm is much less opaque than in many gregarines. The epicyte is thick, transparent and of even width throughout except at the constriction in the middle of the deutomerite where it becomes considerably thicker. Longitudinal striations are easily discernible in the epicyte. The myonemes are well developed, especially at the constriction and in the region of the septum, and are indicated by a series of delicate somewhat reticular fibrillae embedded in the peripheral layer of the endocyte and running crosswise of the body. The nucleus is visible in vivo; it is spherical and in diameter two thirds the width of the body just back of the deutomerite constriction. It lies just posterior to this constriction. One large karyosome is visible within.

The epimerite evidently persists after its usefulness is over, and was seen in one instance on a fairly large specimen free in the lumen of the intestine. It is a large hyaline smooth knob with a short stalk broad at the base.

Neither sporozite nor cyst was seen.

The parasite is fairly active. Gliding motion, accompanied by no bodily contortion was observed at rates of 11 and 7μ per second. Each rate was fairly constant for the given gregarine for a period extending over several minutes. A contortion of the body is common, either with no displacement of the body as a whole or in connection with the gliding motion. In fact, it was difficult to find an animal in simple progression which was not at the same time performing some sort of contortion. The region of the septum is very motile. Here the epicyte expands and contracts, with an inflow or withdrawal of the endocyte, just as in the case of an amoeba. Tiny processes can be seen extruded several at a time or a large portion of the endoplasm of the region may be pushed out one at a time. In the latter case, the heavy and rigid proto-

merite is overbalanced and drops to one side. Immediately thereupon an outpushing of protoplasm on the other side either restores the normal condition or causes a nodding to the opposite side. This movement may continue with surprising rapidity and extend over a long period of time. The deutomerite above its median constriction is very motile, but the portion below is never involved in violent contortions.

This species is similar in general outline to *Stenophora nematoides* Léger and Duboscq (1903a:335-7). Both have the peculiar and hitherto unique constriction at the middle of the deutomerite. They differ in the shape of the protomerite, which in Léger and Duboscq's species is much longer than wide; in the shape of the nucleus, which in *S. nematoides* is elongate ovoidal and in *S. diplocorpa* is spherical; and in the character of movement. I have in no case observed the nematoid shape which is assumed by *S. nematoides* and is due to the elongation of the body and the entire disappearance of the constriction. Motion in *S. diplocorpa* is confined chiefly to regions above the constriction and the latter never entirely disappears.

A table of measurements follows, in which all dimensions are given in microns:

Total length of body	297	325	262	335	359
Length of protomerite	19	20	12	15	14
Length of deutomerite	278	305	250	320	345
Width of protomerite	20	20	20	15	15
Width of deutomerite	45	57	40	45	45
Ratio					
length protom.: total length	1:16	1:16	1:22	1:22	1:25
width protom.: width deutomerite	1:2.2	1:2.8	1:2	1:3	1:3
Diameter nucleus	20	22	18	22	24

CNEMIDOSPORA LUTEA Schneider

[Figures 56 and 57]

1882 *Cnemidospora lutea* Schneider 1882:446-8

Cnemidospora: Sporonts solitary, elongate. Total length 500μ. Width not given. Ratio length protomerite : total length :: 1 : 15; width protomerite : width deutomerite :: 1 : 1.6. Protomerite subglobular, broader than long, in the ratio of 4 : 3. Divided into two parts, the anterior the shape of a double convex lens, without the characteristic endocyte granules, and tinted greenish; the posterior, larger, portion containing yellow or brown endoplasmic granules. Deep constriction

at septum. Deutomerite cylindrical, tapering very slightly and ending in a broad flattened extremity. Endocyte of deutomerite brown, rather dense. Nucleus ellipsoidal, twice as long as wide, containing one or more karyosomes. Myocyte apparent. Cysts not described. Spores ellipsoidal, with a thick integument.

Taken at Poitiers, France. Host: *Glomeris* sp. Habitat: Intestine.

There is but one species in this genus. Crawley (1903a:638-9) described a species as *Cnemidospora spiroboli* but it has been removed to the genus Stenophora, because it has none of the characters of the present genus.

AMPHOROIDES POLYDESMI (Léger) Labbé

[Figure 58]

1892	*Amphorella polydesmi*	Léger	1892:132-4
1899	*Amphoroides polydesmi*	Labbé	1899:20
1903	*Amphoroides polydesmi*	Léger and Duboscq	1903a:314

Amphoroides: Sporonts solitary, ovoidal, rather short and broad. Length 170 – 200μ. Width not given. Ratio length protomerite : total length :: 1 : 20; width protomerite : width deutomerite :: 1 : 26. Protomerite very short, depressed and cup-shaped within. Three times as broad as high. Widest at top, where it is wider than the deutomerite just below septum. A constriction at septum. Septum pushed up in the middle to form a dome which is higher at its summit than the protomerite itself, the latter appearing as a crenulate collar about it. The deutomerite is cylindrical through the anterior third, widening appreciably to form a shoulder, below which it gradually tapers, ending in a broad flattened extremity of approximately the same width as the anterior third of the deutomerite. The endocyte is yellow-brown, the nucleus spherical, its diameter as great as the width of the base of the deutomerite and contains one large karyosome. The epimerite is a cylindroconical or globular papilla. Cysts are spherical, 150μ in average diameter, dehisce by simple rupture and the spores are biconical, 7.8 by 3.8μ.

Taken in the valleys of the Vienne and the Loire, France, and at Vizzanova and Corte, Corsica. Hosts: *Polydesmus complanatus* (L.); *Polydesmus dispar* Silvestri. Habitat: Intestine.

This species was first described by Léger as *Amphorella polydesmi.* The generic name was preoccupied and Labbé changed the name to Amphoroides. At the same time Labbé included with *A. polydesmi* as a synonym *Gregarina polydesmivirginiensis* of Leidy, probably because of the identity of the generic name of the hosts. The character of the

protomerites alone would radically differentiate the two species. The latter has since been named *Stenophora polydesmi.*

Labbé says of the Antinocephalidae, to which the genus Amphoroides belongs the members are parasites of the

"tube digestif d'Arthropodes carnaissere"

but the diplopod Polydesmus is surely not carnivorous.

AMPHOROIDES CALVERTI (Crawley) Watson

[Figure 52]

1903	*Gregarina calverti*	Crawley	1903:48
1903	*Gregarina calverti*	Crawley	1903a:638
1915	*Amphoroides calverti*	Watson	1915:30

Amphoroides: Sporonts solitary, elongate. Maximum length 1670μ, average length 1400μ, average width 120μ. Ratio length protomerite : total length :: 1 :47; width protomerite : width deutomerite :: 1 :2.5 to 1 : 3. Potomerite greatly compressed in sporonts, shallow, five times as wide as high. Deep crater within the top. Constriction at septum sharp and deep. Deutomerite elongate, widest in anterior third, tapering to a sharp point. Endocyte of protomerite tan in color, not dense; of deutomerite opaque, white. Nucleus small, spherical, not visible in vivo. Myocyte well developed. Cysts spherical, 380μ in average diameter. Dehiscence by simple rupture. Spores not known.

Taken at Wyncote, Pa., and Urbana, Ill. Host: *Callipus lactarius* (Say); *Lysiopetalum lactarium* (Say). Habitat: Intestine.

This species was described by Crawley (1903) as belonging to the genus Gregarina. Later (1903a) he described the cysts and spores as follows:

"Cysts spherical – – – 250 – 360μ in diameter. – – Dehiscence effected by sporeducts, from 4 to 8 in number, not exceeding in length the diameter of the cyst. – – – Spores doliform, 13 by 5μ. A single thick spore wall. – –"

I have seen one cyst from this species which measured 380μ in diameter and indicated dehiscence by rupture and not by spore ducts. Crawley probably confused the cysts of this species with those of another which may have been developing in the damp chamber at the same time.

This gregarine bears no resemblance to the members of the genus Gregarina whose cysts dehisce by spore ducts, either in its habitat, in a diplopod, or in any of the characteristics of the sporont. The elongate shape, character of movement by slow contortions, great size of the individual, and chiefly the fact that all the animals are solitary tend to prove conclusively that this species is not a member of the genus Gregarina. I

think that when the unauthentic species have all been properly placed, it will ultimately be shown that members of the genus Gregarina are all associative during the greater part of their adult sporont life. I place this species in the genus Amphoroides because of the shape of the protomerite.

Appendix to the Stenophoridae

Two and only two species have been described as Stenophoridae which are not parasites in diplopods. These are *Stenophora erratica* (Crawley) (1907:220-8) and *S. gimbeli* Ellis (1913:462-5). The former was placed in this family on very slender evidence, viz.: At the anterior tip of the protomerite is a

> "low papilla within which are traces of a pore. It is this character which led me to place the gregarine in the genus Stenophora."

The author notes later the following (1907:221):

> "The suggestion is permissible that this form is actually the common *Stenophora julipusilli* Leidy, somewhat altered in appearance from being in the wrong host. Crickets and Julidae frequently occur in the same environment, and the former might readily swallow the spores derived from the feces of the latter. This done, the spores might readily develop, although producing slightly atypical gregarines."

The present writer has placed the species in a new genus and called it *Leidyana erratica* (Crawley). For argument relative to this position, see under this species, among the Orthopteran parasites.

Ellis (1913) described from a beetle a parasite he calls *Stenophora gimbeli.*

> "The epicyte of the apex of the protomerite is quite thin and the sarcocyte of this region is driven into a papilla which results from the expansion of the thin epicyte."

Such a papilla has been found nowhere else among the Stenophoridae except in *S. cockerellae.* The present writer has often observed an expansion of the epicyte at the apex of the protomerite after the animal has been on the slide for some time in a water medium and it is due to osmosis and the expansion of the epicyte at its weakest point. This gregarine has been removed from the genus Stenophora and placed in the genus Gregarina. The name now stands *Actinocephalus gimbeli.*

With this disposition of the above two species, the family Stenophoridae is found nowhere outside of the family Diplopoda and the diplopods are parasited almost but not exclusively by the Stenophoridae. It is interesting to note in this connection the fact that very rarely is the same species of gregarines found in more than one species of host. Each species of diplopod may be expected to yield its specific parasite, although this is not without exception.

The species of parasites among the Stenophoridae do not appear to be as widely distributed, i. e. as cosmopolitan, as do those of other gregarines, e. g. of the genus Gregarina, widely separted localities seemingly yielding different parasites from the same host or from closely allied hosts. It is true, however, that much less work has been done in different parts of the world on the diplopod parasites than on those of the beetles and Orthoptera.

One is led to believe that each family of gregarines has its unique order or narrowly restricted orders of insects which it infects and that each genus of gregarine is confined to a single host or to very closely related species.

POLYCYSTID GREGARINES IN THE CHILOPODA*

Name of Parasite	Name of Host
DACTYLOPHORIDAE	
Dactylophorus robustus Léger	*Cryptops hortensis* Leach
	Cryptops anomalons lusitanus Verh.
Nina gracilis Grebnecki	*Scolopendra cingulata* (Latr.)
Nina giardi (Léger) Sokolow	*Scolopendra oraniensis*
Nina giardi corsicum (Léger and Duboscq) Sokolow	*Scolopendra oraniensis lusitanica* Verh.
Nina indicia Merton	*Scolopendra subspinipes* Leach
Echinomera hispida (Schneider) Labbé	*Lithobius forficatus* Linn.
	Lithobius coloradensis Cock.
Echinomera horrida (Léger) Watson	*Lithobius calcaratus* Koch
Acutispora macrocephala Crawley	*Lithobius forficatus* Linn.
Trichorhynchus pulcher Schneider	*Scutigera forceps* (Raf.)
	Scutigera sp.
Rhopalonia geophili Léger	*Himantarium gabrielis* Linn.
	Stigmatogaster gracilis Mein.
Rhopalonia stella Léger	*Himantarium gabrielis* Linn.
ACTINOCEPHALIDAE	
Actinocephalus striatus Léger and Duboscq	*Scolopendra cingulata* Latr.
Actinocephalus dujardini Schneider	*Lithobius forficatus* Linn.
Amphorocephalus amphorellus Ellis	*Scolopendra heros* Giard
Hoplorhynchus actinotus (Leidy) Crawley	*Scolopocryptops sexspinosus* (Say)
Hoplorhynchus scolopendras Crawley	*Scolopendra woodi* Meinert
SPECIES OF UNCERTAIN DETERMINATION	OTHER SPECIES UNNAMED
Trichorhynchus lithobii Crawley	

*The parasites are arranged in chronological order under each genus.

DACTYLOPHORUS ROBUSTUS Léger

[Figure 29]

1887	*Dactylophorus* sp.	Schneider	1887:67
1889	*Dactylophorus* sp.	Balbiani	1889:41
1892	*Dactylophorus robusta*	Léger	1892:124-7
1899	*Dactylophorus robustus*	Labbé	1899:17
1903	*Dactylophorus robustus*	Léger and Duboscq	1903:310-1

Dactylophorus: Sporonts solitary, elongate. Length 700 – 800μ. Width not given. Ratio length protomerite : total length :: 1 : 30. Width protomerite : width deutomerite :: 1 : ½. Protomerite at top approximately twice as wide as deutomerite, broadest at top, six times as wide as high. Periphery of upper margin set with numerous small upwardly directed digitiform processes which constitute the epimerite. Deutomerite elongate, regularly cylindrical in anterior third then becoming much narrower and ending in a long acuminate point. Nucleus ovoidal, twice as long as wide, containing several karyosomes. Endocyte yellow. Cysts spherical, 200μ in diameter, dehiscence by pseudocyst, spores cylindrical, rounded at ends, 11 by 4.3μ.

Taken at Grenoble, France, and on the island of Corsica. Hosts *Cryptops hortensis* Leach; *Cryptops anomalons lusitanus* Verh. Habitat: Intestine.

Labbé (1899:17) attributed the naming of the genus Dactylophorus to Balbiani. The latter, however, says:

"C'est d'abord une Grégarine que je crois nouvelle, à moins qu'elle ne soit l'espèce que M. A. Schneider dit avoir découverte chez les Cryptops, et à laquelle il donne le nom de Dactylophorus – – . C'est sans doute la présence de cet appendice qui à valu à notre espèce le nom Dactylophorus, qui lui a été donné par M. Schneider."

Balbiani described a polycystid gregarine from the digestive tract of *Cryptops* sp. as follows:

"La Grégarine a la forme d'üne massue étroite, étirée en une longue pointe àsa partie postérieure. Sa longueur moyenne est de 0.41 mm. et sa larguer, prise dans la portion renflée du corps, de 0.035 mm. Le segment antérieur ou protomérite est petit, connoidé, et prolongé sur un de ses côtés, en un court appendice obtus dirigé en avant."

Labbé considered this species identical with that later described by Léger as *D. robustus,* probably from the fact that the specimens were taken from the same chilopod (Cryptops). It is evident, however, from

figures of the two species, that they are quite unlike. Balbiani's species lacks the dilated flattened protomerite with its digitiform processes, but has rather a high irregular cylindrical protomerite with an eccentric, conical, forwardly directed projection. Moreover, the deutomerite is quite different in shape from that of *D. robustus* (compare Figures 29 and 47) and the nucleus in the one species is spherical, in the other ovoidal. Balbiani's figure compares favorably with figures of sporonts of *Echinomera hispida* (Schneider) Labbé in the following respects; a) the eccentrically placed cone at the apex of the animal, b) the shape of the protomerite, c) the shape of nucleus. In the case of *E. hispida,* the epimerite persists and the cone is a part thereof. Balbiani's figure shows no epimerite, neither does it indicate the digitiform processes characteristic of the other. For these reasons, I do not wish to regard the two species as identical, but rather to leave the one as indefinitely placed. Its original position is obviously incorrect; and the epimerite which is needed to correctly diagnose it not having been discovered, its correct systematic position cannot be determined. Figure 47 is copied from Balbiani's drawing.

NINA GRACILIS Grebnecki

[Figure 30]

1873	*Nina gracilis*	Grebnecki	1873: ?
1887	*Pterocephalus nobilis*	Schneider	1887:68-9
1909	*Nina gracilis*	Léger and Duboscq	1909:33-68

Nina: Sporonts solitary, very elongate. Length 4 to 5 mm. Width not given. Ratio length protomerite : total length :: 1:26; width protomerite : width deutomerite :: 1 : 0.1. Protomerite bilaterally symmetrical, divided into two equal lobes by a perpendicular constriction, these two lobes widely separated at one extremity to form an upturned cornucopia. The free upper extremity of each lobe bordered with a longitudinal row of short sharp spines, from which project long thread-like filaments. Deutomerite constricted just below septum then dilated slightly, the lower half regularly cylindrical, and terminating in a short bluntly pointed extremity. Nucleus slightly ovoidal with several small karyosomes. Csyts spherical. Spores regularly ellipsoidal with one integument, united in chains diagonally.

Taken at Poitiers and at Grenoble (?), France. Hosts: *Scolopendra cingulata* Latr. *(S. cingulata* var. *hispanica* Newp.). Habitat: Intestine.

Labbé (1899:17) says Kölliker's (1849:35) *Gregarina scolopendra*, from *Scolopendra morsitans* Sieb. is probably the same gregarine as the above. But the protomerite is very different from that of the genus Nina and indicates at once Labbé's error. Kölliker gives no description of the epimerite and it is impossible to say in what genus his specimen should be placed. His drawing is reproduced in my Figure 48.

Léger and Duboscq recognize the species and fully discuss its cyst formation.

NINA GIARDI (Léger) Sokolow

1899	*Pterocephalus Giardi*	Léger	1899:390-3
1900	*Nina giardi*	Sokolow	1911:281

Nina: Sporonts solitary, elongate. Length 4 mm. Width not given. Protomerite very broad at the upper extremity, bilaterally symmetrical, consisting of two long parallel horizontal lobes separated at one extremity and upturned at the other, with a small vesicular body near this end. Each lobe set with a row of short upwardly directed teeth from which project long slender sinuous filaments. Deutomerite long, slender, cylindrical, tapering slightly at the posterior extremity and ending bluntly. Cysts spherical. Spores with two envelopes, 14 by 7μ.

Taken at Wimereux, Pas-de-Calais, France. Host: *Scolopendra oraniensis (africana* Verh.) Habitat: Intestine.

NINA GIARDI CORSICUM (Léger and Duboscq) Sokolow

[Figure 31]

1903	*Pterocephalus Giardi corsicum*	Léger and Duboscq	1903a:333
1911	*Nina giardi corsicum*	Sokolow	1911:281-2

Nina: Sporonts solitary, very elongate. Length 2μ. Width not given. Ratio length protomerite : total length :: 1 :10. Ratio width protomerite : width deutomerite :: 4.5 : 1. Protomerite bisymmetrical, formed by two long horns which meet at one end and curve upward nearly 90°. Very wide, 4.5 times maximum width of deutomerite. Extending beyond the deutomerite three times as far on one side as on the other. The periphery of the horns densely set with a row of small denticles with long slender filaments. The shorter lobes thick and blunt. A pseudo-nuclear vacuole near the apex of the opposite lobe, i. e. at the end of fusion. Protomerite transparent. Deutomerite regularly

cylindrical, tapering slightly and ending bluntly. Nucleus large, spherical. Cyst and spores not known.

Taken on the island of Corsica. Host: *Scolopendra oraniensis lusitanica* Verh. Habitat: Intestine.

This species differs from *N. giardi* type only in that a) it attains but half the length of the former, b) the confluent lobes of the protomerite are upturned further in the adult, and c) the lobes of the protomerite are shorter and blunter.

NINA INDICIA Merton

[Figure 33]

1911	*Nina indicia*	Merton	1911:119-26

Nina: Sporonts solitary, elongate. Length $500\mu - 1500\mu$. Width not given. Ratio length protomerite : total length :: 1 : 20; width protomerite : width deutomerite :: 4 : 1. Protomerite bilaterally symmetrical, low and very broad, eight times as wide as high, formed of two long sinuous narrow plates separated at one end for a very short distance. Each bearing a narrow ridge at the upper margin set on both sides with short sharp teeth. The two ridges never confluent but nearly parallel throughout their length. Deutomerite elongate, irregularly cylindrical, dilated a short distance below the septum and tapering from the middle to a long slender and pointed posterior extremity. Endocyte dense in deutomerite, much less dense in protomerite. A deeply staining vesicle at one end of protomerite. Nucleus spherical with chromatin arranged in one convoluted band. Cyst and spores not described.

Taken at Heidelberg, Germany. Host: *Scolopendra subspinipes* Leach. Habitat: Intestine.

ECHINOMERA HISPIDA (Schneider) Labbé

[Figure 32]

1875	*Echinocephalus hispidus*	Schneider	1875:293-4
1899	*Echinomera hispida*	Labbé	1899:16

Echinomera: Sporonts solitary, obese. Measurements not given in the literature. Ratio length protomerite : :total length :: 1 : 7 to 1 : 11; width protomerite : :width deutomerite :: 1 : 2 to 1 : 2.4. Protomerite broad, flattened, surmounted by a persistent epimerite in the form of an irregular asymmetrical cone as broad at its base as the proto-

merite and terminating in an eccentrically placed point. Sides of this cone set with eight digitiform, upwardly directed processes. Deutomerite regularly ellipsoidal, widest in the anterior half or nearly globular, terminating in a broadly rounded extremity eight to ten times the length of the epimerite and protomerite together. Endocyte dense, finely granular, with spherical karyosomes. Cysts are described in the literature as spherical, dehiscence by simple rupture. Spores elongate cylindrical, united in chains. Dimensions not given.

Taken at Paris, France; Cambridge, Mass.; Wyncote, Pa.; Raleigh, N. C.; and Boulder, Colo. Hosts: *Lithobius forficatus* Linn. *(L. forcipatus)* and *Lithobius coloradensis* (Cock.) Habitat: Intestine.

Crawley (1903:52) found this gregarine rather common in *Lithobius forficatus* in eastern United States, and Ellis (1913:465) found it in the West. Neither gives figures of the species. Since Schneider gave no dimensions, these writers based their determination on a comparison of their material with his figures. Ellis gives these measurements: length 180μ, width 80μ. He says

"– – processes of the epimerite disappearing shortly after the animal frees itself from the intestinal wall of the host, but the conical part – – – persists in the sporont stage, giving a symmetrical margin to the front of the protomerite."

"In some specimens the ratio of the length of the protomerite to the length of the deutomerite was as low as one to seven, while Schneider's original figures give it as one to eleven or more. Other specimens seemed intermediate between *E. hispida* (Schn.) and *E. horrida* (Léger). It seems probable then that *E. horrida* (Léger) is synonomous with *E. hispida,* leaving a single species in this genus."

That Ellis found the ratio of length protomerite : length deutomerite as low as 1 : 7 is not out of harmony with Schneider's proportions of *E. hispida,* for the latter says

"Deutomérite huit à dix fois environ plus long que le segments superieure réunis – – –."

E. horrida is much more nearly globose than such proportions indicate and there is no good argument for considering the two species synonymous.

Half a dozen specimens of *Lithobius forficatus* were examined at Oyster Bay, L. I., in October, 1915 and three of them were found to be parasitised with this species. (Figs. 270, 272). From ten to fifty adult parasites were found in the intestine of each host. This species is readily recognized by its intense black color. The specimens are small, the maximum length seen being 330μ, and the maximum width

120μ. The ratio of length protomerite : total length was 1 : 7 and the ratio of width protomerite : width deutomerite was 1 : 2. The sporonts are solitary, and characterized by the possession of a short eccentric conical projection from the protomerite, which is slightly mobile. The protomerite is constricted conspicuously in a horizontal direction at about its middle portion. The protoplasm above this constriction is sparse and transparent; below, it is a little more dense and tan; in the deutomerite it is very dense and black, and the nucleus is not visible.

Cysts were found to be ovoidal in shape and measured 320 by 270μ. Spores were not seen. A table of measurements in which all dimensions are in microns is given here:

Length sporont	330	330	270
Length protomerite	40	50	40
Length deutomerite	290	280	230
Width protomerite	50	60	60
Width deutomerite	120	120	120
Ratio			
length protom.: total length	1:8.2	1:6.6	1:7
Width protom.: width deutomerite	1:2.4	1:2	1:2

ECHINOMERA HORRIDA (Léger) Watson

1899	*Echinocephalus horridus*	Léger	1899:390-5
1911	*Echinocephalus horridus*	Sokolow	1911:281
1916	*Echinomera horrida*	Watson	(This paper)

Echinomera: Sporonts ovoidal, almost spherical, 100-150μ in length. Width not given. Protomerite in shape of a narrow elongate blunt cone, the apex eccentric and carrying a papilla which represents a primitive epimerite. Cysts spherical or cylindrical, rounded at ends.

Taken at Wimereux, France. Host: *Lithobius calcaratus* Koch. Habitat: Intestine.

ACUTISPORA MACROCEPHALA Crawley

[Figure 34]

1903	*Acutispora macrocephala*	Crawley	1903a:632-3

Acutispora: Sporonts solitary, elongate. Maximum length 600μ, width not given. Ratio length protomerite : total length :: 1 : 3; width protomerite : width deutomerite :: 1 : 1.3. Protomerite one-

third the length of the sporont. Conical papilla at apex, deep constriction in posterior third and a constriction of equal depth at septum. Deutomerite just behind septum wider than protomerite just in front of it, regularly conical, tapering from shoulder to a blunt point. Endocyte dense. Nucleus not visible. Cysts spherical, 410μ in diameter, dehiscence by pseudocyst. Spores navicular, slightly curved, slender, two integuments, thin and blunt refractile rod of endocyte at each end, 6μ long; spores 19 by 4μ.

Taken at Raleigh, N. C. Host: *Lithobius forficatus* L. Habitat: Intestine.

The genus Acutispora was created by Crawley for this unique species.

TRICHORHYNCHUS PULCHER Schneider

[Figures 35, 36]

1882	*Trichorhynchus insignis*	Schneider	1882:439-42
1882	*Trichorhynchus pulcher*	Schneider	1882:439-42
1889	*Gregarina megacephala*	Leidy	1889:10-11
1899	*Trichorhynchus pulcher*	Labbé	1899:16

Trichorhynchus: Sporonts solitary, elongate, length 420 to 750μ; width 240μ. Ratio length protomerite : total length :: 1 : 4 to 1 : 7. Width protomerite : width deutomerite : 1 : 1 to 1 : 1.6. Epimerite nearly half the total length of body without it. Protomerite conical, rounded at summit. Slight constriction at septum. Deutomerite just below septum same width as protomerite just above it, widest in anterior third. Constricted below middle portion then dilated and ending in a broad but sharply pointed cone. Epimerite a very long flexible 'tongue' proceeding from the apex of the protomerite, slightly dilated at the extremity. Endocyte in both parts dense. Nucleus ovoidal with one large karyosome. Cysts ovoidal, 316 by 303μ. Dehiscence by pseudocyst. Spores cylindrical, rounded at ends, 9.7 by 5.8μ.

Taken at Poitiers, France; Philadelphia, Pa. Hosts: *Scutigera*, sp.; *Scutigera forceps* (Raf.) *(Cermatia f.)*. Habitat: Intestine.

This gregarine was described by Schneider under the name *T. insignis*, but his references to his plates are to figures of *T. pulcher*. It was probably an error in the proof which was accountable for the incorrect naming of the species, for the name of the species immediately preceding is *Lophocephalus insignis*.

Labbé referred to the species as *T. pulcher*.

Crawley referred the gregarine which was described by Leidy as *G. megacephala* (Fig. 35) to the present species because of the elongate appendage on the protomerite. That this position is correct is attested by the fact that Crawley himself found the species, the specimens agreeing with Schneider's figures and with the dimensions as given by Leidy. Crawley's description is as follows:

"This form is well described by A. Schneider whose figure also is excellent, giving a very accurate idea of the actual animal. Schneider, however, gives no dimensions, while Leidy says that the dimensions vary from 420 to 750 microns, these figures agreeing very closely with those which I obtained.

"My own observations on this species show it to be an active, very polymorphic gregarine, with the ability to undergo extensive alterations in shape. Thus, the anterior end of the protomerite, normally a blunt curve, frequently protrudes in a long tongue-shaped process. The peristaltic movement so frequently displaced by gregarines, may, in this species, pass forward as well as backward. This indicates that here the contractile elements are capable of operating as well in one direction as another, which is certainly not the case in most polycystid gregarines. Fusion, preparatory to encystment, was seen to take place 'head to head.'"

Leidy's brief account of the species is as follows:

"One morning – – I found a fine *Cermatia forceps* in my bedroom. It was – – species which may be named *Gregarina megacephala.* The body is elongated ovate and acute or short clavate and obtuse with an unusually large ovoid and often constricted head, surmounted by a small rounded or elongated appendage. Length 0.42 to 0.75 mm. by 0.24 broad; head about one-fourth the length of the body. It approximates *Dufouria agilis* of Schneider, found in the larvae of a Hydracantharis."

The latter species lacks the elongated proboscis; it is now known as *Legeria agilis* (Schn.) Labbé. For description and drawing, see chapter on Coleoptera.

RHOPALONIA GEOPHILI Léger

[Figure 51]

1894	*Rhopalonia geophili*	Léger	1894:1285-88
1896	*Rhopalonia geophili*	Léger	1896:29

Rhopalonia: Sporonts solitary, dicystid, obese. Widest at anterior end, tapering to a point. Length 500μ. Epimerite a large hyaline subspherical plate with a corona of ten to fifteen backwardly directed digitiform processes placed above the protomerite on a short neck. Endocyte with large yellow-orange granules. Nucleus ovoidal, containing several karyosomes. Cysts spherical, 200 to 250μ, the fertile half brown, the sterile half white, a black equatorial band marking the future

line of dehiscence. Spores cylindrical, rounded at ends, double walled, 16 by 6.5μ.

Taken in Provence, France and on the island of Corsica. Hosts: *Himantarium gabriclis* Linn. *(Geophilus g.); Stigmatogaster gracilis* Meinert. Habitat: Intestine.

This parasite is peculiar in having no septum in the adult sporont and thus no protomerite and deutomerite. A rudiment of a protomerite is indicated by a finely granular yellow mass at the proximal end of the body, separated from the rest of the sporont by a clear area. Léger thinks this genus is transitional between the Cephalina and the Acephalina. His words are as follows:

"La Grégarine est donc, au point de vus èvolutif, une dicystidée vraie, c'est-a-dire n'ayant jamais plus de deus segments; auu apparail de fixation caduc et un segment unique persistants (pseudo-monocystis) representant à la fois le protomérite et le deutomérite des tricystidés. Elle se rapproche en cela des grégarines intestinales des vers marine."

Léger and Duboscq (1903:311) found a parasite on the island of Corsica which may be the *Rhopalonia geophili* of Léger.

"Les Stigmatogaster d'Ajaccio contenaient dans leur intestin de rares sporadin en forme de toupie, surmountés au pôle antérieur d'un plateau circulaire bordé d'un bourrelet saillant. Nous les rapportons avec quelque doute an *Rhopalonia geophili* Léger, fréquent dans les *Stigmatogaster gracilis* de Provence et dont les sporadins sont généralement de forme plus allongée."

RHOPALONIA STELLA Léger

1899 *Rhopalonia stella* Léger 1899:390-5

Rhopalonia: Sporonts solitary, ovoidal, elongate or spindle shaped. Length about 130μ, width not given. Body not differentiated into protomerite and deutomerite. The epimerite is like that of *R. geophili* Leger and " – – rapelle assez bien une fleur de syanthérés." (Sokolow 1911 :281).

Host: *Himantarium gabriclis* Linn. Habitat: Intestine.

The comparison of the epimerite with the flower of one of the Compositae is a good one, as seen in Figure 51.

ACTINOCEPHALUS STRIATIUS Léger and Duboscq

[Figure 37]

1903 *Actinocephalus striatus* Léger and Duboscq 1903a:334-5

Actinocephalus: Sporonts solitary, minute. Length 30–35μ. Width not given. Ratio length protomerite : total length :: 1 : 4; width protomerite: width deutomerite :: 1 :.7. Protomerite wider than deutomerite, dome shaped, broadly rounded in front with a small flattened circular papilla surrounded by a circle of small teeth. Constriction at septum, which is curved upward. Deutomerite irregularly cylindrical, terminating in a sharp cone. Epicyte marked with very apparent longitudinal striations, from whence the name. Nucleus ovoidal with its longitudinal axis perpendicular to that of the body. Cyst and spores unknown.

Taken in Provence, France. Host: *Scolopendra cingulata* Latrielle. Habitat: Intestine.

This gregarine is placed in the genus Actinocephalus from the character of the dentate papilla of the protomerite.

"– – – au sommet du protomérite fait saillie un petit bouton aplati, à bord régulièrement festonné, comme dentelé, au centre dupuel s'élève un rostre mobile asset droit. C'est là l'epimérite qui, comme on le voit, présente de grandes analogies avec celui des Actinocephalus."

ACTINOCEPHALUS DUJARDINI Schneider

[Figures 38, 39, 40]

1875 *Actinocephalus dujardini* Schneider 1875:589-90

Actinocephalus: Sporonts solitary, rather obese. Length and width not given. Ratio length protomerite : total length :: 1 : 2.4; width protomerite : width deutomerite :: 1 :1. Protomerite very large, cylindrical, longer than wide, nearly one third total length of sporont, terminating in a truncated cone, the apical region being hyaline, slight constriction at septum. Deutomerite widest just behind the septum and tapering gradually to a sharp point. Endocyte of equal density in protomerite and deutomerite. Epimerite a globose sessile body resting on the apex of the protomerite, drawn out in its apical region to a short neck upon which is set a flat corona of 16 to 20 backwardly directed rigid spines. Nucleus small, spherical. Cyst and spores not known.

Taken at Paris, France. Host: *Lithobius forficatus* Linn. *(L. forcipatus)*. Habitat: Intestine.

Crawley (1903:55) records finding this little gregarine several times in *L. forficatus*. He gives no drawings and does not state where it was taken.

AMPHOROCEPHALUS AMPHORELLUS Ellis

[Figures 45, 46]

1913	*Amphorocephalus amphorellus*	Ellis	1913:463-4

Amphorocephalus: Sporonts solitary, elongate, length 500 to 970μ, width not given. Ratio length protomerite : total length :: 1 : 1.7; width protomerite : width deutomerite : 1 : 2.5. Protomerite dome shaped, broadly rounded in front, a distinct constriction near middle. Deutomerite cylindrical, tapering slightly to a sharp point. Endocyte dense, nearly black. Epimerite flask-shaped with fluted apical disc, sessile on the protomerite, persisting on large free cephalonts. Nucleus not noted. Cyst and spores not seen.

Taken at Boulder, Colo. Host: *Scolopendra heros* Giard. Habitat: Intestine.

This genus contains the unique species above. It is characterized by the flask-shaped epimerite with finger-like processes at the apex and by the protomerite having a constriction at the middle, extending horizontally around the same.

HOPLORHYNCHUS ACTINOTUS (Leidy) Crawley

[Figures 42, 43]

1899	*Gregarina actinotus*	Leidy	1889:10
1903	*Hoplorhynchus actinotus*	Crawley	1903:55-56
1913	*Amphorocephalus actinotus*	Ellis	1913b:277

Hoplorhynchus: Sporonts solitary. Maximum length recorded that of Leidy, 520μ, maximum width 80μ. Crawley's maximum recorded length, 485μ, width 105μ. Ratio length protomerite : total length :: 1 : 9 (Leidy) to 1 : 12 (Crawley); width protomerite : width deutomerite :: 1 : 2 (Leidy and Crawley). Protomerite dome shaped, twice as broad as high. Deutomerite roughly triangular, wider than protomerite at septum. Attaining maximum width at shoulder, thence tapering to a more or less sharp point. Epimerite 80 to 100μ long, vase shaped, broadest near base and tapering to a neck where it again widens into a broad disc of short digitform processes from 8 to 20 in number. Crawley says:

"– – amphora shaped. Differentiated in front into four dichotomously branched lobes. – – In the small animals making up nearly 1/2 the total length; in the adults from 1/4 to 1/5 of the total length."

Endocyte dense and opaque. Nucleus ovoidal, diagonally placed. Cyst and spores not known.

Taken at Philadelphia, Wyncote and Wallingford, Pa., and Raleigh, N. C. Hosts: *Scolopocryptops sexspinosus* (Say) and *Scolopocryptops* sp. Habitat: Intestine.

Crawley (p. 56) says:

"Apparently in this gregarine the septum tends to disappear. It is much more evident in some cephalonts than in others, and in one sporont seen no septum could be made out, and the endocyte of the protomerite was not distinguishable from that of the deutomerite."

Ellis (1913b) placed this gregarine in his genus Amphorocephalus. He characterizes the genus as follows:

"Protomerite with a constriction near the middle dividing it into two lobes, the anterior of which is the smaller; epimerite longer than wide, but not extremely elongate, widest in its posterior third, narrowed at its junction with the protomerite terminating in a somewhat concave enlargement, the edge of which has a fluted appearance because of the presence of numerous small finger-like processes; deutomerite elongate."

It is readily seen that the species in question does not fit this generic diagnosis for the following reasons: 1) the protomerite is not constricted in the middle, with a small anterior part; 2) the epimerite is elongate, from two to four times as long as wide (in Ellis' described species it is but little longer than wide, 1 : 1.2); 3) the apex does not terminate in a broad disc, the edge of which has a fluted appearance, because of the presence of numerous small finger like processes, but terminates in a disc edged with dichotomously branched distinctly separated digitiform processes, from eight to twenty in number; 4) the deutomerite is not elongate as in Ellis' figure, in which it is from eighteen to twenty-two times the length of the protomerite, but is only from six to twelve times the length of the protomerite. I have therefore replaced the species in the genus designated by Crawley.

HOPLORHYNCHUS SCOLOPENDRAS Crawley

[Figure 41]

1903	*Hoplorhynchus scolopendras*	Crawley	1903a :636-7
1913	*Amphorocephalus actinotus*	Ellis	1913b :277

Crawley's description of the species is quoted:

"This species is created for a gregarine parasitic in *Scolopendra woodi* Meinert from Raleigh, N. C. Two specimens were present. One of these, when first

seen, was a balloon-shaped sac, 350μ long by 200 broad. The epicyte and sarcocyte were each nearly or quite 3μ thick, and the former was plainly marked with longitudinal striations. Both of the individuals were very flexible, readily changing shape and showing extensive contortions. After having been upon the slide for perhaps an hour, the parasites became quiescent and assumed what was probably something like the typical shape. The larger then measured 825μ long by 120 broad. The anterior end, as shown in figure 19, was much narrower than the balance of the animal, but it is somewhat questionable if this narrowing is permanent. A distinct septum extended across this narrower region, cutting off a portion of granular entocyte. Backward from the broadest portion, the animal's body tapered gradually, ending behind in a point. This species is placed in the genus Hoplorhynchus on account of its close resemblance to *H. actinotus* Leidy and its occurrence in a centipede related to Scolopocryptops, the host of the latter."

Its position is doubtful from insufficient evidence and will not remain authentic unless corroborated and described in more detail by some future worker.

Ellis included this species with *H. actinotus* under the name *Amphorocephalus actinotus* (Leidy). I have referred the species to the original position. The protomerite does not have the constriction necessary to place it in the genus Amphorocephalus.

SPECIES OF UNCERTAIN DETERMINATION

TRICHORHYNCHUS LITHOBII Crawley

[Figure 44]

Crawley's statement (1903a:637) concerning this species is as follows:

"This animal, which is apparently specifically distinct from any other gregarine parasitic in Lithobius, was found in a specimen of that centipede from Raleigh, N. C. An epimerite was not found. The protomerite was subcordiform, and displayed in front a differentiation the exact nature of which could not be determined. The deutomerite varied considerably in shape, the animal being quite polymorphic. Both epicyte and sarcocyte were distinct and of about equal thickness. The septum was thick and curved backward. The endocyte was not dense; the nucleus large, with several karyosomes. The largest individual seen was 195μ long."

There seems to be no basis for placing the parasite in the named genus. None of the characteristics of the genus are named above, the elongate epimerite, ovoidal cysts which dehisce by pseudocyst, cylindrical spores. Enough data are lacking so that the species cannot be definitely placed in any genus.

A parasite is described by Léger and Duboscq (1903a:312) but not named. It was found on the island of Corsica, in *Chaetechelyne vesuviana* Newport. Their statement in full follows:

"Sur plusieurs individis examinés, un seul (d'Ajaccio) était parasité par une Grégarine recontrée seulement au stade de sporadin. Sous cette forme, la Grégarine est allongée et mesure 100μ. Le deutomérite est, dans sa partie antérieure, plus large que le protomérite dont il atteint 5 ou 6 fois la longuer, puis il va en s'atténuait pour se terminer en pointe pousse. Ces caractères ne sont pas suffisants pour rapporter ces sporadins à un Rhopalonia plutôt qu' à un Actinocephalus."

A third species of indeterminate situation is that called by Balbiani *Dactylophorus* sp. (1889:41). This species has been discussed in detail under the heading *Dactylophorus robustus* (Léger) Labbé, and is illustrated in Figure 47.

A fourth species of doubtful position is that described by Kölliker as *Gregarina scolopendra* (Figure 48). See discussion under *Nina gracilis* Grebnecki.

POLYCYSTID GREGARINES IN THE ORTHOPTERA*

Name of Parasite	Name of Host
GREGARINIDAE	
Gregarina oblonga Dufour	*Oeipoda stridula*
	Oedipoda migratoriae
	Gryllus campestris
Gregarina hyalocephala Dufour	*Tridactylus variegatus*
Gregarina ovata Dufour	*Forficula auricularia* L.
Gregarina blattarum Siebold	*Periplaneta orientalis* (L.)
	Periplaneta americana (L.)
	Blatella germanica (L.)
Gregarina locustae Lankester	*Dissosteria carolina* (L.)
Gregarina oviceps Diesing	*Gryllus abbreviatus* Serv.
	Gryllus americana Blatch.
Gregarina macrocephala (Schn.) Labbé	*Nemobius sylvestris* (F.)
	Gryllus domesticus (L.)
Gregarina panchlorae Frenzel	*Panchlora exoleta* Klug
Gregarina acridiorum Léger	*Tryxalis* sp.
	Pamphagus sp.
	Sphingonotus sp.
Gregarina paranensis (Kunckel d' Hercularis) Watson	*Schistocera paranensis*
Gregarina serpentula deMagalhaes	*Periplaneta orientalis* (L.)

*The parasites are arranged in chronological order under each genus.

Gregarina rigida (Hall) Ellis	*Melanoplus differentialis* (Uhler)
	M. femur-rubrum (deGeer)
	M. atlanis (Riley)
	M. coloradensis ?
	M. bivitattus (Say)
	M. angustipennis (Dodge)
	M. femoratus (Burm.)
	M. luridis (Dodge)
	Hesperotettix pratensis Scudder
	Schistocera americana Burm.
	Brachystola magna Giard
	Encoptolophus sordidis (Burm.)
Gregarina kingi Crawley	*Gryllus abbreviatus* Serv.
Gregarina longiducta Ellis	*Ceuthophilus latens* Scudder
	C. maculatus (Say)
Gregarina consobrina Ellis	*Ceuthophilus valgas* Scudder
Gregarina illinensis Watson	*Ischnoptera pennsylvanica* (deGeer)
Gregarina galliveri Watson	*Gryllus abbreviatus* Serv.
Gregarina stygia Watson	*Ceuthophilus stygius* (Scudder) L.
Gregarina nigra Watson	VARIOUS ACRIDIDAE
Gregarina udeopsylla Watson	*Udeopsylla nigra*
Leidyana erratica (Crawley) Watson	*Gryllus abbreviatus* Serv.
	Gryllus pennsylvanica Burm.
Leidyana gryllorum (Cuénot) Watson	*Gryllus domesticus* (L.)
Hyalospora roscoviana Schneider	*Petrobius maratimus*
Hyalospora affinis Schneider	*Machilus cylindrica* E. Geoff.
Gamocystis tenax Schneider	*Blatella laponica*
Hirmocystis gryllotalpa (Léger) Labbé	*Gryllotalpa gryllotalpa* (L.)
ACTINOCEPHALIDAE	
Pileocephalus blaberae (Frenzel) Labbé	*Blabera clarziana* Sauss.
Actinocephalus fimbriatus (Diesing) Ellis	*Dissosteria carolina* (L.)
INDETERMINATE SPECIES	
Gregarina conica Dufour	*Coleoptera* and *Gryllus*
Gregarina davini Léger and Duboscq	*Gryllomorpha dalmatina* Ocsk.
MISCELLANEOUS	
Gregarina sphaerulosa Dufour	
Gregarina soror Dufour	

GREGARINA OBLONGA Dufour

[Figures 177, 178]

1837	*Gregarina oblonga*	Dufour	1837:13
1848	*Gregarina oblonga*	Frantzius	1848:195
1851	*Gregarina oblonga*	Diesing	1851:11
1863	*Gregarina oblonga*	Lankester	1863:94

The only description extant is the original one of Dufour, which is as follows:

"Oblonga flavescens conico-cylindroidea; cephalothorace abdominis quintam partem vix adeaquante.

Hab—Oedipodae migratoriae et Grylli campestris.

Beaucoup moins conique la G. conique elle a une couleur jaunâtre qui ne s'observe pas dans les autres espèces."

Here, as in the case of *Gregarina conica,* Dufour confused more than one species under a single name. Oedipoda is a genus of the order Diptera and also of the Orthoptera. If the Dipteran order is meant, the same species of gregarine would not be looked for in both Diptera and Orthoptera. Such an instance has not yet been recorded for a single species.

Dufour's drawings from both insects are, however, similar and are reproduced in my Figures 177 and 178, although the protomerites are slightly different in their relation to the deutomerites.*

Frantzius lists the species as from Oedipda only. He places it in the same genus Gregarina "stets zu zwei aneinander geheftet."

Diesing mentions it with hosts as *Oedipoda migratoria* and *O. stridula,* and from *Gryllus campestris.*

Lankester gives the host as Gryllus. After this mention, the species passes out of the literature. I have listed it among the parasites of the genus Gregarina because Dufour states

"cephalothorace abdominis quintam partem"

and because Frantzius lists it among the parasites with both primite and satellite.

This species may be identical with *Gregarina macorcephala* Schn. from the identity of one of the hosts, but the two cannot be correlated. Dufour describes only sporonts and Schneider only cephalonts and un-

*I have not attempted to separate the parasite in the two hosts as two species from the meager description we have, but have recorded this species in this chapter as well as in Part III, a list of Polycystid Gregarines, under the Diptera.

til the cephalonts of the former or the sporonts of the latter or both will have been described, the two species must remain separate.

The only other parasite described from a host belonging to the subfamily Oedipodinae (Acrididae) is *Gregarina locustae* Lankester, but the sporonts of the two species are not identical.

The second host named is now known as *Nemobius sylvestris* (F.).

GREGARINA HYALOCEPHALA Dufour

[Figures 181, 182]

1837	*Gregarina hyalocephala*	Dufour	1837:13
1851	*Gregarina hyalocephala*	Diesing	1851:11
1863	*Gregarina hyalocephala*	Lankester	1863:94
1899	*Gregarina hyalocephala*	Labbé	1899:34

Dufour's description is as follows:

"Oblongo-conica; cephalothorace hemispherico diaphano, abdominis quartam partem subadaequante – –. Hab. in ventriculo Tridactyli."

The species is, from this description, and from the character of the epimerite (Figure 182) quite evidently a member of the genus Gregarina.

Frantzius does not mention the species; Diesing and Lankester merely do so and Labbé places it among his Uncertain Species.

GREGARINA OVATA Dufour

[Figure 183]

1826	*Gregarina ovata*	Dufour	1826:18
1837	*Gregarina ovata*	Dufour	1837:12
1837	*Gregarina ovata*	Siebold	1837:408
1838	*Clepsidrina conoidea*	Hammerschmidt	1838:356
1845	*Gregarina ovata*	Desmarest	1845:?
1848	*Gregarina ovata*	Frantzius	1845:95
1851	*Gregarina ovata*	Diesing	1851:10
1863	*Gregarina ovata*	Lankester	1863:94
1873	*Clepsidrina ovata*	Schneider	1873:515-33
1885	*Clepsidrina ovata*	Schneider	1875:578-9
1875	*Clepsidrina ovata*	Schneider	1885:?
1899	*Gregarina ovata*	Labbé	1899:10
1904	*Gregarina ovata*	Pachler	1904:14-18
1905	*Clepsidrina ovata*	Schnitzler	1905:309

Gregarina: Sporonts biassociative. Measurements not given in any description. Ratio length protomerite : :total length primite : :

1 : 5 to 1 : 6; width protomerite : width deutomerite :: 1 2. Protomerite of primite hemispherical, slightly constricted at septum. Protomerite of satellite flattened. Deutomerite ovoidal, widest below middle in primite, above middle in satellite. Posterior end rounded. Nucleus spherical with many small karyosomes, visible in vivo. Epimerite a simple hyaline knob.

Cysts spherical or slightly ovoidal, dehiscence by sixteen, more or less, spore ducts; spores cylindrical, truncate at ends (not barrel shaped), macrospores and microspores (15.8 by 7.9; 8.3 by 3.7μ).

Taken in France, and in Berlin and Danzig, Germany. Host: *Forficula auricularia* L. Habitat: Intestine.

Dufour designated as hosts *Gryllus campestris* and *Forficula*. He gave a good figure of biassociative sporonts taken from Forficula, and a figure of a single sporont from Gryllus which differs considerably in shape from the other and probably represents another species, although I have not attempted to place it systematically.

Siebold accidentally found this species in Forficula but he did not think the organisms were animals, for no motion was observed.

Frantzius represented an accurate figure of the species. He named Forficula as host, recognizing Dufour's error in including a parasite from Gryllus.

Diesing indicated that Hammerschmidt had described a synonymous species, *Clepsidrina conoidea*, from the same host. He also included as a synonym *G. psocorum Sieb.* but from the fact that the host, *Psocus quadripunctatus,* is a Neuropteran, I doubt the authenticity of this statement. Siebold's paper is not available and the conjecture cannot be verified.

Schneider agreed with Diesing that *Clepsidrina conoidea* is a synonym of *Gregrina ovata*. He discussed at length (1873) the cyst formation in this species. In 1885, he worked upon the species in greater detail, finding and giving measurements of two kinds of spores.

The species was the subject of a monograph by Paehler in 1904.

I have examined about fifty specimens of *Forficula auricularia* L. at Cold Spring Harbor, L. I., without finding parasites.

GREGARINA BLATTARUM Siebold

[Figure 184]

1839	*Gregarina blattarum*	Siebold	1839:57
1848	*Gregarina blattarum*	Stein	1848:223
1848	*Gregarina Blattarum*	Frantzius	1848:193,195
1851	*Gregarina Blattarum*	Diesing	1851:10
1853	*Gregarina Blattae orientalis*	Leidy	1853:239
1863	*Gregarina blattarum*	Lankester	1863:94
1875	*Clepsidrina blattarum*	Schneider	1875:580
1881	*Gregarina blattarum*	Bütschli	1881:384-409
1891	*Gregarina blattarum*	Wolters	1891:115-24
1893	*Gregarina blattarum*	Marshall	1893:25-45
1899	*Gregarina blattarum*	Labbé	1899:10
1900	*Clepsidrina blattarum*	deMagalhaes	1900:38-44
1903	*Gregarina blattarum*	Crawley	1903:44
1907	*Gregarina blattarum*	Hall	1907:149
1913	*Gregarina blattarum*	Ellis	1913b:265
1913	*Gregarina blattarum*	Ellis	1913c:83-84

Gregarina: Sporonts biassociative, rather stout bodied, more or less irregular in outline. Length of sporonts 450 to 500μ. Width 185 to 200μ. Ratio length protomerite : total length primite :: 1 : 5; width protomerite : width deutomerite :: 1 : 2. Protomerite of primite cylindrical in posterior two thirds, rounded anteriorly, no constriction at septum. Very little wider than high. Protomerite of satellite flattened, wider than protomerite of primite, twice as wide as high. Deutomerite irregularly cylindrical, widest in posterior half of primite and in anterior half of deutomerite. More or less pointed at posterior extremity. Sarcocyte layer thick. Nucleus small, spherical, (44μ in diameter—deMagalhaes—) with from four to six karyosomes. Epimerite a simple hyaline knob.

Cysts spherical or ovoidal. Spore ducts reach to outside of transparent cyst cover. Spore ducts 8 to 10 in number. Spores cylindrical to barrel shaped, truncate at ends, 8.5 by 3.7 and 4 by 8μ.

Taken at Danzig, Berlin, Heidelberg, Bonn, and Leipsic, at Paris, at Philadelphia, Pa. and at Rio Janeiro, Brazil. Hosts: *Periplaneta orientalis* (L.) *(Blattae or.); P. americana* (L.); *Blatella germanica* (L.) *(Ectobia germ.)*. Habitat: Intestine.

This is a remarkably cosmopolitan species, as seen from the locations where it was taken. It is remarkable also in that the name has remained almost undisputed since its discovery.

Leidy described briefly *Gregarina blattae orientalis* from the United States, which species proved to be synonymous with the earlier named species, coinciding in measurements, proportions and host.

Schneider gave a brief description, with good figures of an association and of a dehiscing cyst.

Bütschli admirably described the process of cyst formation from beginning to end, a process never before seen and very rarely described since.

Wolters observed some of the nuclear changes in the cyst.

Marshall contributed the third long paper on development.

deMagalhaes found the species in Brazil in 1900; three years later Crawley found it in the United States, both from the original host. The specimens found by these workers were undoubtedly those of the true old-world *G. blattarum*. The shape and proportions correspond, and in hosts of the nature of the cockroach, there is little wonder that both host and parasites are widely distributed.

GREGARINA LOCUSTAE Lankester

[Figure 188]

1853	*Gregarina Locustae Carolinae*	Leidy	1853:239
1856	*Gregarina Locustae Carolinae*	Leidy	1856:47
1859	*Gregarina fimbriata*	Diesing	1859:730
1863	*Gregarina Locustae*	Lankester	1863:94
1899	*Gregarina locustaecarolinae*	Labbé	1899:35
1903	*Stephanophora locustaecarolinae*	Crawley	1903:54
1907	*Gregarina locustaecarolinae*	Crawley	1907:225
1913	*Gregarina locustaecarolinae*	Ellis	1913b:268

Gregarina: Sporonts biassociative. Maximum length of sporonts 350μ, average length 250μ. Ratio length protomerite : total length primite :: 1 : 6.8; width protomerite : width deutomerite :: 1 : 1.7. Protomerite a little more than hemispherical, one and one half times as wide as high. Deutomerite cylindrical, rather square cornered posteriorly, nearly twice as wide as the protomerite. Nucleaus large, spherical, with one karyosome. Epimerite a small rounded knob with a very short neck.

Taken at Philadelphia and Wyncote, Pa. Host: *Dissosteria carolina* (L.) Habitat: Intestine.

Crawley recognized (1907) the fact that Leidy described and illustrated two distinct species under the same name. Leidy's figures 35 and 36 (1853), the former my figure 188, represent isolated sporonts typical of the genus Gregarina in relative strength and width of proto-

merite and deutomerite. Associations were not mentioned, however. His figure 37 (Figure 189) is quite different in shape and the epimerite is an inverted campanular structure furnished with slender upwardly directed digitiform processes. Because of the epimerite, Crawley (1903) placed the species in the genus Stephanohora. In 1907, he found cephalonts in locusts quite unlike those seen by Leidy. They possessed simple knobbed epimerites like those of other species of the genus Gregarina. He saw the sporonts also, and they compared favorably in length with those described by Leidy. At the same time, Crawley substantiated Leidy's discovery of the digitform epimerite, for he found similar cephalonts and also sporonts which compared. Thus it was discovered that two species were involved, the one a true Gregarina, the other not. The latter species is now known as Actinocephalus fimbriatus (Diesing) Ellis.

The name of the species as given by Leidy is a trinominal and cannot stand. The first binominal name applied to the species was that of Lankester, which must be used to designate the species. The name used by Diesing, *Gregarina fimbriata,* applies to the species *Actinocephalus pachydermus* for he says proboscis "digitato-fimbriata".

GREGARINA OVICEPS Diesing

[Figures 191, 192]

1853	*Gregarina Achetae abbreviatae*	Leidy	1853 :238
1856	*Gregarina Achetae abbreviatae*	Leidy	1856 :47
1859	*Gregarina oviceps*	Diesing	1859 :730
1863	*Gregarina Achetae*	Lankester	1863 :94
1899	*Gregarina achetaeabbreviatae*	Labbé	1899 :35
1903	*Gregarina achetaeabbreviatae*	Crawley	1903 :45
1903	*Gregarina achetaeabbreviatae*	Crawley	1903a :639
1907	*Gregarina achetaeabbreviatae*	Crawley	1907 :220-1
1913	*Gregarina achetaeabbreviatae*	Ellis	1913b :266
1915	*Gregarina achetaeabbreviatae*	Watson	1915 :34

Gregarina: Sporonts biassociative, obese. Maximum length 500μ. Average sporonts 450μ in length, 225μ in width. Ratio length protomerite : total length primite :: 1 : 3; width protomerite : width deutomerite :: 1 : 1.1. Protomerite hemispherical to subglobose, width twice the height. Slight constriction at septum. Deutomerite stout-bodied, nearly as wide as long. Widest at shoulder where it is very little wider than protomerite. Posterior end truncate. Epimerite undescribed. Endocyte dense in deutomerite, less so in protomerite. Nucleus not visible

in vivo and not seen. Cysts spherical, 250μ in average diameter. Spore ducts 2 to 5, of maximum length 1000μ. Spore barrels shaped, 4.5 by 2.25μ.

Taken at Haverford and Philadelphia, Pa., Beach Haven, N. J., Douglas Lake, Mich., Urbana, Ill., Oyster Bay, L. I. Hosts: *Gryllus abbreviatus* Serv. *(Achcta abbreviata); G. americanus* Blatch. Habitat: Intestine.

Leidy's drawing of the species (1853), my figure 191, represents the same gregarine as that described by later writers. But later drawings from Leidy's unpublished manuscript, Crawley's 1903 paper (Pl. III, Figs. 34, 35), show two distinctly different species, one associative and the other not. Crawley confused the two in his description, under the name *Gregarina achetacabbreviatae.* In 1907 he described two distinct species, however, one the *Gregarina achetaeabbreviatae* of Leidy and a new *Stenophora erratica,* for the solitary species. The latter I have transferred to a new genus Leidyana. For description, see under *L. erratica.*

Ellis found this species at Douglas Lake, Mich., and I have found it from material taken at Haverford, Pa., Urbana, Ill., and Oyster Bay, L. I.

Diesing changed the name of Leidy's species to *Gregarina oviceps* without giving explanation therefor and since this is the oldest binomial name used, the species must bear this name.

GREGARINA MACROCEPHALA (Schneider) Labbé

1875	*Clepsidrina macrocephala*	Schneider	1875:674
1882	*Clepsidrina macrocephala*	Schneider	1882:442
1887	*Clepsidrina macrocephala*	Schneider	1887:73
1895	*Clepsidrina* sp.	Cuénot	1895:321
1897	*Clepsidrina gryllorum*	Cuénot	1897:54
1899	*Gregarina macrocephala*	Labbé	1899:10

Gregarina: Sporonts biassociative.

The following synopsis refers to the cephalont only, there being no available description of the sporont.

Ratio length protomerite : total length primite :: 1 : 5; width protomerite : width deutomerite :: 1 : 1.2. Protomerite rounded laterally, as wide as high. Constriction at septum. Epimerite superimposed upon protomerite on a short stout neck. Epimerite a large hyaline ovoidal body a little longer than the protomerite of the cephalont. Deutomerite elongate cylindrical, tapering suddenly to a sharp

point. Endocyte with large irregularly arranged protoplasmic granules. Cysts spherical, dehiscing by spore ducts. Spores doliform.

Taken in Aisne, Indre-et-Loire, and Vienne, France. Hosts: *Nemobius sylvestris* (F.) *(Gryllus s.); Gryllus domesticus* L. Habitat: Intestine.

In 1875 Schneider merely mentioned the character of the epimerite of the undescribed species. In 1882 he described the cephalont only.

This species may be identical with *Gregarina oblonga* Dufour, from the same host. It is impossible, however, to correlate the two species for the reason that Dufour described only sporonts and Schneider only cephalonts.

Leidyana gryllorum (Clepsidrina g.) was erroneously included with this species by Labbé. For discussion, see under *L. gryllorum.*

GREGARINA PANCHLORAE Frenzel

[Figure 187]

1892 *Gregarina panchlorae* Frenzel 1892:290-300

Gregarina: Sporonts biassociative, long and slender. Sporonts 180μ long, 35μ wide. Protomerite of satellite cylindrical, constricted slightly in anterior half. Deutomerite of primite fits into a deep depression in anterior end. Deutomerite cylindrical. Nucleus spherical, 18 to 20μ in diameter, with one karyosome.

Taken in Cordoba, Argentina. Host: *Panchlora exoleta* Klug. Habitat: Intestine.

Frenzel gave a meagre description and but one drawing of this species, illustrating only the manner in which the protomerite of the satellite fits into the deutomerite of the primite. This part of the association is intermediate between that of the same portion of *G. serpentula* deMagalhaes, as shown in his two figures, the one of a young, the other of a mature, association. (Figs. 185 and 186.) The lengths of the two species are, however, widely at variance so the species are not identical.

GREGARINA ACRIDIORUM Léger

1893	*Clepsidrina acridiorum*	Léger	1893:811-13
1896	*Clepsidrina acridiorum*	Léger	1896:27-30
1899	*Gregarina acridiorum*	Labbé	1899:10

Gregarina: Sporonts biassociative, cylindrical. Maximum length of individual 1000μ; minimum length 400μ, width 160μ. Ratio length protomerite : total length :: 1 : 5; protomerite subglobular in primite, depressed at anterior end in satellite. Deutomerite cylindrical, rounded at posterior end. Sarcocyte thick, especially in protomerite near septum. Endocyte yellow orange. Epicyte longitudinally striated. Myocyte well developed. Nucleus spherical, with many small karyosomes. Epimerite a simple spherical hyaline button on a short stalk.

Cysts spherical, 500μ in diameter. Spore ducts 12 to 15 in number, very long, yellow orange at base. Spores extruded in long chains. Spores doliform, 7.6 by 3.3μ.

Taken at Nemours, Algeria, and in Provence, France. Hosts: Various Acrididae, especially *Tryxalis* sp. *(Truxalis), Pamphagus* sp. and *Sphingonotus* sp. Habitat: Intestine.

GREGARINA PARANENSIS (Kunckel d'Hercularis) Watson

1899	*Clepsidrina paranensis*	Kunckel d'Hercularis	1899:622
1916	*Gregarina paranensis*	Watson	(This paper)

Gregarina: Sporonts biassociative. Length not given. Deutomerite four times as long as protomerite. Ellipsoidal, pale yellow.

The author says the species differs from *G. acridiorum* Léger in having the deutomerite ellipsoidal instead of cylindrical, and the endocyte pale yellow instead of yellowish red. He says between the moults of the insect the parasites are abundant. They diminish in number after each moult.

Taken at Parana, Argentina. Host: *Schistocerca paranensis.* Habitat: Intestine.

GREGARINA SERPENTULA deMagalhaes

[Figures 185, 186]

1900	*Gregarina serpentula*	deMagalhaes	1900:140-44

Gregarina: Sporonts biassociative, slender, elongate. Maximum length association 1200μ, width 180μ. Average length 800μ, width 60μ.

The protomerite is 50μ long. Ratio length protomerite : total length :: 1 : 8; width protomerite : width deutomerite :: 1 : 1.3. Protomerite subspherical, flattened at septum, width equal to length. Constriction at septum. Deutomerite elongate cylindrical broadly rounded behind. Nucleus spherical with several karyosomes. Young associations more slender, protomerites greatly attenuated. Cysts spherical or ovoidal.

Taken at Rio Janeiro, Brazil. Host: *Periplaneta orientalis* (L.). Habitat: Intestine and coelom.

de Magalhaes names the species *serpentula* from the manner of movement.

"– a m'ont paru rappeler la forme de la tête d'un serpent et ses mouvements."

The author found instances in which more than two sporonts were attached:

"Celli-ci (espèce) fournit fréquement des examples d'association de plusieurs invidis disposes en file; deux trois et plus sont accolés par leurs extrémités opposées. D'autres fois, ils forment des groupes constitues d'un plus gros exemplaire, à l'extrémité postérieure duquel sont accolés deux, trois, cinq satellites plus petits."

These phenomena are observed in rare instances throughout the genus Gregarina.

This species is quite distinct in characteristics from *G. blattarum* Sieb., from the same host and its authenticity is not questioned.

GREGARINA RIGIDA (Hall) Ellis

[Figures 194, 197, 198, 271, 290-333, 336-338]

1907	*Hirmocystis rigida*	Hall	1907:149-174
1907	*Gregarina melanopli*	Crawley	1907:223
1913	*Gregarina rigida*	Ellis	1913b:267
1913	*Gregarina melanopli*	Ellis	1913c:82-3
1915	*Gregarina rigida*	Watson	1915:34-35

Gregarina: Sporonts biassociative, rather stout bodied. Maximum length of association 1425μ, average length 550μ. Sporonts 250 to 750μ long, 130 to 210μ wide. Ratio length protomerite : total length :: 1 : 3 to 1 : 6 (primite); length protomerite : total length (satellite :: 1 : 5 to 1 : 16; width protomerite : width deutomerite :: 1 : 1.4. Protomerite somewhat flattened, width sometimes three times the height, generally less. Constriction at septum more or less indistinct. Deutomerite cylindrical or barrel shaped, little wider than protomerite, ending in a broadly rounded or flattened square cornered extremity.

Endocyte very dense and brownish yellow in deutomerite, tan in protomerite. Epimerite a small spherical hyaline knob.

Cysts yellow orange, 300μ in average diameter, spore ducts short, ten or more in number. Spores extruded in chains, barrel shaped, 5 by 8μ.

Taken at Wyncote, Pa.; Douglas Lake, Mich.; Lincoln, Neb.; Colorado Springs, Colo.; Boulder, Colo.; Urbana, Ill.; and Oyster Bay, L. I.

Hosts *Melanoplus femoratus* (Burm.); *M. luridis* (Dodge); *M. femur-rubrum* (de Geer); *M. atlantis* (Riley) *(M. atlantis); M. differentialis* (Uhler); *M. coloradensis* ? ; *M. angustipennis* (Dodge); *Encoptolophus sordidis* (Burm.); *Schistocerca americana* Burm.; *M. bivitattus* (Say); *Hesperotettix pratensis* Scudder; *Brachystola magna* Giard. Location: Intestine and caeca.

This species was first described by Hall as *Hirmocystis rigida.* He mentioned dehiscence of the cysts by simple rupture, and he saw neither the spores nor the epimerite. The only character in common with the genus Hirmocystis was the simple rupture of the cysts, and this character is possessed by some thirty genera.

Crawley (1907) published an article two months later describing a new species, *Gregarina melanopli,* which proved to be the same species. He found that dehiscence occurred by means of numerous spore ducts. The epimerite was still unknown.

Ellis changed the name of the species to *Gregarina rigida* (Hall).

I have taken parasites of this species from various Acrididae in material from Colorado Springs, Lincoln, and Urbana. In three instances specimens were recovered from *M. femur-rubrum* at Oyster Bay, L. I. (Fig. 271). Although hundreds of grasshoppers have been examined at the latter place, infection has been found but these few times, and then very few parasites were present. Cysts have developed, all with numerous long spore ducts. Typical spores were extruded.

GREGARINA KINGI Crawley

[Figure 193]

1907	*Gregarina kingi*	Crawley	1907:221-3
1913	*Gigaductus kingi*	Ellis	1913b:271

Gregarina: Sporonts biassociative, rather stout bodied. Maximum length of associations 350μ. Sporont measurements not given. Ratio length protomerite : total length :: 1 : 3; width protomerite : width deutomerite :: 1 : 1. Protomerite saddle-shaped, i.e. broadly dilated and nearly flattened apically, with deep constriction just below middle,

dilated again less extremely below. Widest part twice the width of narrowest part. Protomerite equal in length to its greatest width, a slight constriction at septum. Deutomerite widening out rapidly from septum to shoulder, and quite regularly cylindrical from thence downward. Very broadly rounded at distal end. Nucleus spherical, small. Endocyte not dense.

Cysts spherical, 110μ in maximum diameter, one spore duct only, spores barrel shaped, 5 by 2.75μ in dimensions.

Taken at Wyncote, Pa. Host: *Gryllus abbreviatus* Serv. Habitat: Intestine.

Ellis placed the species in question in the genus Gigaductus, originally created by Crawley himself for *Gigaductus parvus.* I have allowed this genus to drop out, removing the type species to the genus Gregarina, for its differentiating character was the large single spore duct. A discussion of the matter is found in the chapter on Coleoptera, under the species *Gregarina parva.*

This species has been replaced in the genus to which it was originally assigned.

GREGARINA LONGIDUCTA Ellis

[Figure 195]

1913 *Gregarina longiducta* Ellis 1913c:78-82

Gregarina: Sporonts biassociative, obese. Length of associations 800 to 900μ. Ratio length protomerite : total length primite :: 1 : 3.5; width protomerite : width deutomerite :: 1 : 1. Protomerite broadly rounded in front, widest through middle, twice as wide as high, and deeply constricted at septum. Deutomerite slightly broader than high, barrel shaped, widest through middle. Very broadly rounded or flattened at posterior end. Satellite longer than primite in all associations observed. Nucleus not seen. Endocyte very dense, black. Epimerite a short digitiform process equal in length to protomerite of cephalont.

Cysts spherical, 560μ in average diameter. Spore ducts 3 to 3.5 mm. in length, four in number, arranged around one pole of cyst. Spores discharged in chains. Cylindrical, 3 by 6.5μ.

Taken at Douglas Lake, Mich. Hosts: *Ceuthophilus latens* Scudder and *C. maculatus* (Say). Habitat: Intestine.

GREGARINA CONSOBRINA Ellis

[Figure 196]

1913 *Gregarina consobrina* Ellis 1913b:267

Gregarina: Sporonts biassociative, obese. Average length of sporonts 600μ, average width 450μ. Ratio length protomerite : total length primite :: 1 : 3.5 to 1 : 4; width protomerite : width deutomerite :: 1 : 1.5. Protomerite hemispherical, no constriction at septum. Deutomerite subspherical to ovoidal, nearly or quite as wide as long, broadly rounded posteriorly. Endocyte not described. Nucleus not seen. Epimerite short, simple, digitiform.

Cysts 250 to 300μ in diameter. Spore ducts 4 to 6, all in one hemisphere, 900 to 1200μ in length. Spores extruded in chains, cylindrical, 3.2 by 8μ.

Taken at Boulder, Colo. Host: *Ceuthophilus valgas* Scudder. Habitat: Intestine.

GREGARINA ILLINENSIS Watson

[Figure 207]

1915 *Gregarina illinensis* Watson 1915:34

Host: *Ischnoptera pennsylvanica* (de Geer).

This species was taken at Urbana, Ill., in November, 1914. The intestine of one field cockroach was found to contain twenty-five associations. A dozen or more immature specimens of the insect were collected at various times throughout the fall but only the one was infected.

The sporonts are biassociative and elongate cylindrical in shape. The maximum length of an association seen was 1110μ, length of the primite being 550μ, its width 180μ. Ratio length protomerite : total length primite :: 1 : 5; width protomerite : width deutomerite :: 1 : 1.1 to 1 : 1.5. The protomerite of the primite is dome shaped, the width equalling the height. The widest part of the primite is the middle portion. There is a constriction, not very deep, at the septum. The protomerite of the satellite is rectangular in shape, 1.5 times as wide as high and depressed at the anterior end into which concavity the primite fits. The deutomerite is regularly cylindrical, elongate and well rounded at the posterior end. The nucleus is large and spherical, and contains many small chromidia. The endocyte is dense in both

protomerite and deutomerite and is black in transmitted light. The nucleus is not visible in vivo.

Cephalonts and cysts were not recovered from the host.

A table of measurements in which all dimensions are given in microns follows:

Total length association	1110	1110	1080	1050
Primite				
Length protomerite	100	100	100	90
Length deutomerite	450	450	440	410
Width protomerite	130	130	110	110
Width deutomerite	170	180	180	170
Total length sporont	550	550	540	500
Ratio				
length protom.: total length sporont	1:5.5	1:5.5	1:5.4	1:5.5
width protom.: width deutomerite	1:1.3	1:1.4	1:1.7	1:1.5
Satellite				
Length protomerite	70	130	80	70
Length deutomerite	530	430	440	480
Width protomerite	130	130	130	120
Width deutomerite	190	210	170	180
Total length sporont	560	560	520	550
Ratio				
length protom.: total length sporont	1:8	1:4.3	1:6.5	1:8
width protom.: width deutomerite	1:1.5	1:1.6	1:1.3	1:1.5

This species and the Old World *Gregarina blattarum* Sieb. of *Blatta orientalis* are differentiated as follows:

	G. blattarum	*G. illinensis*
Shape	Irregularly cylindrical	Very regularly cylindrical
Posterior end satellite	Not well rounded, often pointed	Well rounded always
Sarcocyte	Very thick	Thin except in protomerite
Shape protomerite of satellite	Flattened, wider at base than elsewhere 1.7 times as wide as at top, 2.5 times as wide as high	But slightly flattened, as wide at base as at top, 1.5 times as wide as high

In the following characteristics, the two species agree:

Ratio		
length protom.: total length primite	1: 5	1: 5
length protom.: total length satellite	1: 8	1: 8
Shape protomerite of primite	Hemispherical	Hemispherical
Nucleus	Spherical	Spherical

On the strength of the shape of the posterior end of the body, the shape of the satellite, and in the regularity in shape of the body there is basis for the creation of a new species, although in one important factor, proportions, the two species agree. There are no measurements stated for the Old World species. Schneider says "– – elle devient trés-volumineuse" which indicates that the species may be as large as the one here described. The species described by Leidy (1853:239) from *Blatta orientalis* agrees in size with both species. His drawings indicate an irregularly shaped body and a more or less sharply pointed posterior extremity and the hosts he dissected were probably the introduced European cockroach and the gregarine the Old World *G. blattarum.*

Crawley records (1903:44) the species *G. blattarum* as

"Common in *Periplaneta orientalis, P. americana* and *Ectobia (Blatta) germanica.* A few specimens of *Ischnoptera pennsylvanica,* the field cockroach, were examined, but none contained gregarines."

These hosts undoubtedly yielded the same parasites which Leidy also had found at Philadelphia.

Ellis (1913b:83) says:

"This gregarine was found in several specimens of the native roach *Ischnoptera pennsylvanica* from the woods near Douglas Lake. – – Although no introduced roaches have been collected in the vicinity – –, this gregarine from native roaches seemes undoubted the typical *G. blattarum,* agreeing in spores, cysts and sporonts with that species. The biological question of interest is, of course, the source of infection of these native roaches. – – It is possible, however, that *G. blattarum* is established in the native roaches in the new world. – – – both Frenzel and Magalhaes found the native roaches to be infected with gregarines other than *G. blattarum* – – –."

In his Syllabus (1913b:265), Ellis gives measurements which coincide fairly well with those recorded above in the table. The maximum length of a sporont he states to be 520μ, while that of the above species is 560μ. He says

"Cysts prolate spheroids, average 450 x 900μ – –, spore ducts 10 or more, reaching the length of 200μ; sporocysts barrel-shaped, 4 x 8μ,"

Ellis' drawing differs somewhat in shape from that of any specimen seen by the present writer (ratio length protomerite : total length primite in the former 1 : 3.3, in the latter 1 : 5) but this is not sufficient to constitute a new species as it is the only difference in the two. It is highly probable that but one species is involved. Ellis' specimens were taken from *Ischnoptera pennsylvanica* (de Geer) at Douglas Lake, Mich.

Hall (1907) makes the simple statement that *Periplaneta americana* contains *Gregarina blattarum*. I have no reason to doubt its presence.

It is to be noted that the terms *Blatta orientalis* and *Periplaneta o.* are used interchangeably by various authors, the name now accepted being *Blatta orientalis* L.

GREGARINA GALLIVERI Watson

[Figures 205, 275-290]

1915 *Gregarina galliveri* Watson 1915:33-34

Host: *Gryllus abbreviatus* Serv.

This species was taken at Oyster Bay, Long Island, in August, 1914. The parasite lives in the intestine of the host. The species is rare, being seen only three times in a hundred or more crickets opened, sixty-five associations and five cysts being found in a single host, and a dozen or more associations in each of the other two. In the first named, nearly all the associations were engaged in cyst making.

The sporonts are biassociative, even to the smallest seen. The maximum length of an association seen was 590μ, the maximum width 180μ. The animals are quite polymorphic but certain generalizations can be made. The protomerite of the primite is always wider than the deutomerite. Measurements indicate that it is but little wider, but the difference seems much greater because the two places of greatest width, those used in the table of measurements, are widely separated. The protomerite is low and broad, either flat or very slightly rounded at the anterior end and from two to four times as wide as high, the average being three. Its widest part is in the middle, where it is approximately one and a half times as wide as the septum. The protomerite of the satellite is considerably narrower than that of the primite. It is greatly flattened and from two to four times as wide as high. The deutomerite of the primite is constricted a little just below the septum, widening out below the middle where it attains nearly the measured width of the protomerite. In some instances it is nearly cylindrical. The deutomerite of the satellite is irregularly subglobular to broadly

ellipsoidal in shape and is of approximately the same width as the protomerite of the primite. The ratio of length protomerite : total length primite (for twelve associations) remains nearly constant and is approximately the same in the satellite as in the primite, being 1 : 5. The ratio of width protomerite : width deutomerite of primite is approximately 1.5 : 1; in the satellite it is 1 : 1.4.

The endocyte is very dense in both protomerite and deutomerite, and is brown in color, not black as in so many species. The protomerite granules are much larger than those in the other species seen in the same host. The nucleus is small and spherical. It is not visible in vivo except in young individuals.

Upon carefully flattening out the association on the slide, by slight pressure, a large inflated papilla is seen on the anterior end of the satellite, which fits into a corresponding depression in the primite and makes the union firmer. This was well demonstrated in some specimens from a starved host in which the protoplasm of the parasite was pale tan throughout and both the papilla and the nuclei were clearly visible.

The trophozoites possess a knob shaped hyaline epimerite.

Cysts are 300 to 350μ in diameter*, very dense like the sporonts and deep brown in color. In one cricket, all the associations were engaged in cyst making. Two such processes were watched from the incipiency to the completion of the two cysts, and the process took place in less than half an hour. At 11 a. m., five cysts were present on another slide, and at 2 p. m. there were seven. Several of the cysts which when first observed were sporonts, developed to completion with the extrusion of ripe spores. The maximum number of spore ducts seen on a cyst was nine. The ducts are very long. The spores are barrel shaped, 3 by 6μ.

It was anticipated that this species was identical with Crawley's *Gregarina kingi* because of the peculiarly shaped protomerite of that species, but such was found not to be the case; the two species differ in many respects. The following table indicates the chief differences:

*The diameter, exclusive of the transparent layer, is 50μ less.

	G. galliveri	*G. kingi*
Maximum length of association	590μ	350μ
Ratio		
length protom.: total length sporont	1 : 5	1 : 3
width protom.: width deutomerite	1 : 0.8	1 : 1.1
Shape protomerite of primite	Broad and flat, shape slightly irregular three times as wide as high Wider than deutomerite	"Saddle shaped, broad and swollen in front, much narrower behind" Narrower than deutomerite
Shape protomerite of satellite	Flattened, four times as wide as high	"Subspherical to compressed", twice as wide as high
Shape deutomerite of primite	Constricted below septum, dilated below and widest in posterior two-thirds	"Cylindrical, generally broader in front. Outline often irregular"
Shape deutomerite of satellite	Subspherical to broadly ovate	
Nucleus	Spherical, small	Spherical, small
Endocyte	Very dense, deep brown in both protomerite and deutomerite	"Not dense"
Anterior surface of satellite	Provided with a very large, flattened papilla which fits into large depression in primite	Shows a slightly raised ring, primite fitting into a very shallow saucer on anterior end of satellite
Cysts, diameter	350μ	90 to 100μ.
Dehiscence	Many spore ducts	Single long spore duct
Frequency	Rare, not more than one cricket in 40 harboring it	"25% of crickets opened contained these parasites in countless numbers"

No other allied species has been described from crickets.

Measurements of a few associations with all dimensions expressed in microns are as follows:

Total length association	590	570	540	490	440
Primite:					
Length protomerite	60	70	60	60	40
Length deutomerite	230	200	210	210	190
Width protomerite	150	140	170	180	120
Width deutomerite	130	140	150	150	100
Total length sporont	290	270	270	270	230
Ratio					
length protom.: total length	1:5	1:4	1:4.5	1:4.5	1:5.7
width protom.: width deutomerite	1:1.1	1:1	1:1.1	1:1	1:4.1
Satellite:					
Length protomerite	50	50	50	40	50
Length deutomerite	250	250	220	180	170
Width protomerite	110	130	140	120	90
Width deutomerite	150	180	180	170	120
Total length sporont	300	300	270	220	210
Ratio					
length protom.: total length	1:6	1:6	1:5.4	1:5.5	1:4.2
width protom.: width deutomerite	1:1.3	1:1.4	1:1.3	1:1.4	1:1.3
Diameter cysts	350	300	350		

GREGARINA STYGIA Watson

[Figure 206]

1915 *Gregarina stygia* Watson 1915:33

This new species was taken from *Ceuthophilus stygius* (Scudder), hosts found in an unused cistern on Dr. C. B. Davenport's grounds, at Cold Spring Harbor, L. I.

The infection was heavy, as many as five hundred parasites being found in each of several hosts, and each of the twelve examined contained at least a few parasites. The region of infection is the intestine.

The sporonts are biassociative as adults. The longest association measured 360μ. The sporonts are barrel shaped, the maximum length recorded being 180μ and the maximum width 100μ. The protomerite is nearly hemispherical in the primite and is flattened in the satellite. The deutomerite is widest at or in front of the middle portion. The satellite is somewhat more slender than the primite and is of the same length or a little shorter. The endocyte is dark tan in color, not very dense in either deutomerite or protomerite, and the nucleus is easily visible in

vivo. The sarcocyte is thicker at the septum and anterior ends of the protomerite than elsewhere, but is fairly thick throughout. The nucleus is small and spherical and contains one or more large karyosomes.

Sections show that the cephalont possesses a single knobbed epimerite, slightly stalked. The sporozoite is spindle-shaped and contains a large nucleus. Several sporozoites were seen in the sectioned intestine lying free in the lumen or contiguous to the epithelial wall.

Movement is sluggish and of the ordinary two types, gliding and contortion.

Cysts average 150μ in diameter. Dehiscence was not seen.

This species is not identical with *Gregarina longiducta* Ellis (1913a:78-82), from *Ceuthophilus latens* and *C. maculatus*. Associations of the latter average 800 – 900μ in length, the smallest observed being 465μ long. Large associations of *G. stygia* are only 350μ in length. Proportions vary as well as lengths.

The species differs from *G. consobrina* Ellis (1913:267) in size. Sporonts of the latter species attain a length of 600μ, those of *G. stygia* not becoming longer than 180μ.

Satellite:

No other species is recorded from the genus Ceuthophilus.

A table of measurements is appended herewith, all dimensions being given in microns:

Total length associations	360	330	300
Primite:			
Length protomerite	30	20	30
Length deutomerite	150	140	120
Width protomerite	60	40	55
Width deutomerite	100	100	80
Total length sporont	180	160	150
Ratio			
length protom.: total length	1:6	1:8	1:5
width protom.: width deutomerite	1:1.6	1:2.5	1:1.5
Satellite:			
Length protomerite	20	25	30
Length deutomerite	160	145	120
Width protomerite	60	50	70
Width deutomerite	80	60	80
Total length sporont	180	170	150
Ratio			
length protom.: total length	1:9	1:7	1:5
width protom.: width deutomerite	1:1.3	1:1.2	1:1.1

GREGARINA NIGRA Watson

[Figures 210, 333, 334, 335]

1915 *Gregarina nigra* Watson 1915:33

Hosts: *Melanoplus femur-rubrum* (deGeer); *Encoptolophus sordidus* (Burm.).

This parasite seems to be present only as a secondary one. It never occurs in large numbers but is generally found in the same host as *Gregarina rigida*. During the season of 1913, I found the parasite comparatively frequently, but not over half a dozen Acridiidae yielded the species when collections were made in the fall of 1914. It is easily differentiated from the more commonly found species in both color and shape, especially of the protomerite. It was collected only at Urbana, Illinois.

The maximum length of an association found was 1 mm. The ratios of various parts of the body are about the same as for *G. rigida*. The shape of the body is, however, quite different. The protomerite is shaped like a truncated cone; it is widest at the base, flattened on the top and square cornered. It is approximately as high as wide at the base; there is no constriction or only a very slight one at the septum. A slight indentation persists at the apex of the protomerite left by the detachment of the knob-like epimerite. The deutomerite is cylindrical, of the same width throughout and very little wider than the protomerite. It terminates in a broadly rounded extremity. The protomerite of the satellite is often not at all flattened but is little shorter than that of the primite and of approximately the same shape.

The endocyte of the deutomerite is very opaque and dense, being black in transmitted light. The protomerite is somewhat less dense than the deutomerite. The nucleus is not visible in vivo. It is spherical, in diameter about one third the width of the deutomerite and contains many karyosomes. The epicyte is thick at the anterior end of the protomerite, being thin elsewhere.

I have not been able to differentiate the cysts of this species (if present in my collections) from those of *G. rigida*. The size would be about the same, judging from the size of the associations. I have never seen an infection in which this species alone was present so have no way of knowing exactly which species yielded the cysts found when both species are present in an infection. In the instance of every cyst from Acridiidae which I have watched develop, spore ducts grew from small orange colored discs on the surface. The spore ducts were always short and the spores doliform.

A table of measurements follows in which all dimensions are given in microns:

Total length association	990	880	1000
Primite:			
Length protomerite	140	150	150
Length deutomerite	390	290	380
Width protomerite	120	130	140
Width deutomerite	150	170	180
Total length sporont	530	440	530
Ratio			
length protom.: total length	1:3.8	1:3	1:3.5
width protom.: width deutomerite	1:1.2	1:1.4	1:1.3
Satellite:			
Length protomerite	110	100	90
Length deutomerite	350	340	380
Width protomerite	110	120	130
Width deutomerite	170	150	160
Total length sporont	460	440	470
Ratio			
length protom.: total length	1:4.2	1:4.4	1:5.2
width protom.: width deutomerite	1:1.5	1:1.2	1:1.2

GREGARINA UDEOPSYLLAE NOV. SPEC.

[Figures 260, 261]

Host: Udeopsylla nigra (Locustidae). Location, Urbana, Ill.

Three specimens of this rare host were examined and all found to be moderately infected with an hitherto undescribed gregarine. The parasites lay in inert masses in the mid intestine.

The sporonts are biassociative and obese. The maximum observed length for an association was 600μ. The largest primite was 310μ long and 200μ wide. The average ratio of length protomerite : total length sporont was 1 : 5.2, and the ratio of width protomerite : width deutomerite :: 1 : 5. The sporont is elongate ellipsoidal in shape. The protomerite of the primite is slightly longer than wide, widest in the central portion, and terminates in a small cone. There is a deep constriction at the septum. The deutomerite is widest in the middle, and the satellite terminates in a broadly rounded extremity. The protomerite of the satellite is broad and shallow and from two to three times as wide as long. An indentation is present in the anterior end of each protomerite of an association.

The protoplasm is dense, tan in the protomerite and black in the deutomerite. The nucleus is spherical and is visible only in young specimens.

Cysts and the epimerite were not seen.

Some of the more important measurements, with all dimensions given in microns, follow:

Total length association	600	580	500
Primite:			
Length protomerite	60	50	50
Length deutomerite	250	220	200
Width protomerite	100	100	60
Width deutomerite	200	130	110
Length sporont	310	270	250
Ratio			
length protom.: total length	1:5.1	1:5.4	1:5
width protom.: width deutomerite	1:2	1:1.3	1:1.8
Satellite:			
Length protomerite	40	50	50
Length deutomerite	250	260	200
Width protomerite	140	100	80
Width deutomerite	190	120	110
Length sporont	290	310	250
Ratio			
length protom.: total length	1:7.2	1:6.2	1:5
width protom.: width deutomerite	1:1.3	1:1.2	1:1.3

This species differs from *Gregarina longiducta* Ellis in length of the sporonts and in shape of the protomerite; and from *G. consobrina* Ellis in shape and proportions of the protomerite; it differs from *G. stygia* Watson in size and shape.

The hosts from which all these gregarines are taken are various species of the genus Ceuthophilus, which is closely related to the genus Udeopsylla. The parasite in question is readily distinguished from the above species by the cone-shaped protomerite of the primite.

LEIDYANA ERRATICA (Crawley) Watson

[Figures 208, 218-56]

1903	*Gregarina achetaeabbreviatae*	Crawley	1903:45
1907	*Stenophora erratica*	Crawley	1907:221
1915	*Leidyana solitaria*	Watson	1915:35

Hosts: *Gryllus abbreviatus* Serv. and *G. pennsylvanicus* Burm.

The parasites were taken at Cold Spring Harbor and Oyster Bay, L. I., Haverford, Pa., and at Urbana, Illinois, during the summer and fall of 1914.

The intestine is the usual seat of infection, although the pyloric caeca are not infrequently found to contain parasites. The latter are generally present in small or moderate numbers, from 1 to 25 per host, and nearly ever cricket examined at this season was parasitized. Sometimes the number per host runs up to one hundred or more, but this is rare.

The parasites are solitary, never associative in the normal sporont life. The maximum recorded length is 500μ, the maximum width 160μ. The ratio of length protomerite to total length for fifteen specimens is 1:5 to 1:7. The ratio of width is 1 : 1.3 to 1 : 1.7. The protomerite is slightly wider than high. It is broadly cone-shaped, dilated in the middle and constricted at the septum. The constriction is very conspicuous and fairly deep in the adults. There is no papilla at the anterior end. The deutomerite is cylindrical to elongate ellipsoidal, sometimes tapering but always rounded at the end (Figures 218, 221).

The endocyte is very dense and black in the deutomerite (in transmitted light) and pale tan in the protomerite, the two parts being sharply contrasted. Longitudinal striations are easily discernible with the aid of an intra vitam stain or after crushing the body and releasing the dense endocyte (Figure 243). The nucleus is spherical and contains one or two small karyosomes. It is not visible in the dense adults, but is seen in vivo in the younger sporonts and in the trophozoites.

The epimerite is a large simple spherical hyaline knob set upon a short slender stalk (Figures 224, 227). The sarcocyte is very distinctly visible in contrast to the contiguous endocyte. It is thin and of even width throughout.

Trophozoites with epimerites are common, both free in the lumen and attached to the cells of the intestine. They are transparent or nearly so. Some individuals are surprisingly large.

Cysts average 350μ in over all diameter, the transparent envelope being about 30μ in thickness when the cyst is new. Dehiscence is by spore ducts from one to twelve or more in number. Spores are extruded from the long ducts in chains. The spores are barrel-shaped and measure 3 by 6μ.

This species was described by Crawley (1903:45) as *Gregarina achetaeabbreviatae* Leidy and later as *Stenophora erratica*. Crawley first considered the species identical with Leidy's *Gregarina achetaeabbreviatae* from the same host but later (1907:221) created for it a new species because

"– – at the anterior tip of the protomerite the ectosarc is often thickened to form a low papilla, within which are traces of a pore."

It is this character which led him to place the gregarine in the genus Stenophora. He adds:

"The suggestion is permissible that this form is actually the common *Stenophora julipusilli* Leidy, somewhat altered from being in the wrong host – – –".

The suggestion that the species belongs to the family Stenophoridae is excluded when one considers the method of cyst dehiscence, which is that characteristic of the family Gregarinidae rather than that of the Stenophoridae.

The sarcocyte at the anterior end of the protomerite is often thickened and papillate but I have not seen a trace of a pore.

A table of measurements follows, all dimensions being given in microns:

Length sporont	500	490	470	420	370	290
Length protomerite	80	70	80	60	60	50
Width protomerite	110	90	80	80	80	50
Width epimerite						30
Width deutomerite	150	150	160	140	130	60
Ratio						
length protom.: tl. length	1:6.3	1:7	1:6	1:7	1:6.1	1:6
width protom.: width deu.	1:1.3	1:1.7	1:2	1:1.7	1:1.6	1:1.2

LEIDYANA GRYLLORUM (Cuénot) Watson

[Figure 209]

1897	*Clepsidrina gryllorum*	Cuénot	1897:52-54
1900	*Gregarina macrocephala*	Labbé	1899:10
1901	*Gregarina gryllorum*	Cuénot	1901:594-5
1916	*Leidyana gryllorum*	Watson	(This paper)

Leidyana: Sporonts solitary, never associative, cylindrical. Length 420μ. Ratio length protomerite : total length :: 1 : 5; width protomerite : width deutomerite :: 1 : 1.1. Protomerite subspherical, a deep constriction at septum. Deutomerite cylindrical, conical at end. Epimerite globular, nucleus small, spherical. Cysts spherical or ovoidal, 190 to 240μ in diameter. Spore ducts 3 to 8μ. Spores barrel shaped, 7μ in longest axis.

Taken in Ardennes and Meurthe-et-Moselle, France. Host: *Gryllus domesticus* (L.). Habitat: Intestine.

Labbé placed this species which had been mentioned but not described by Cuénot as a synonym of *Gregarina macrocephala* Schn.,

which is only known from the cephalont. Cuénot (1901) says regarding the disposition of the species:

"Labbé – – – l'à réunit de son propre chef à la *G. macrocephala* A. Schn.; or, cette derniere espèce est trop mal connue pour qu'il ait quelque à l'identifier à la mieune; le grand épimérite en forme de massue de 'macrocephala' n'est certainment pas pareil a celui de 'gryllorum.'

In a footnote he adds:

"Schneider ne décrit pas la forme adulte et ne parle pas du nombre de spo-reductes des kystes."

Therefore the species has an individuality. It is very similar to the species described here under the name *Leidyana erratica.* Both are solitary, size of the two is nearly the same, ratios of various parts not radically different and shape of the deutomerite quite similar. The cysts are slightly smaller than in the latter species, but they dehisce by approximately the same number of spore ducts and the spores are similar. The epimerites of the two species are spherical and large. The nuclei are spherical. The only difference seems to be in the shape of the protomerite. In all the hundreds of specimens I have seen of *L. erratica,* none has possessed a protomerite rounded at the anterior end; all have been decidedly conical at the apex. In the present species, the protomerite is broadly rounded—subspherical—in shape; the constriction at the septum is considerably deeper than in the other species. I have separated the two on the basis of this character alone, deeming it of sufficient import to differentiate the species. Both species are parasites of the genus Gryllus, but of different species. The host of the former, *Gryllus domesticus,* flourishes in the old world and is rare in the United States, having formerly been found about old log houses, the former occupants of which undoubtedly introduced it from Europe (Blatchley). The host of *Leidyana erratica, Gryllus abbreviatus,* is the common field cricket in the United States. The infection is unlikely to have spread from the one host to the other.

HYALOSPORA ROSCOVIANA Schneider

For detailed synopsis and discussion of this species, see the chapter on Coleopteran parasites, under the same species name. The host is *Petrobius maritimus,* but as the genus Petrobius has been described for both Coleoptera and Orthoptera, it is impossible to state finally whether the host was a beetle or an orthopteran, or a thysanuran.

HYALOSPORA AFFINIS Schneider

[Figure 200]

1882	*Hyalospora affinis*	Schneider	1882:445-6
1899	*Hyalospora affinis*	Labbé	1899:14

Hyalospora: Sporonts biassociative, slender and elongate. Length of cephalonts 300μ. Sporont measurements not given. Ratio length protomerite : total length primite :: 1 : 5 (without epimerite). Ratio width protomerite : width deutomerite :: 1 : 1.8. Endocyte yellow. Epimerite a hyaline knob, present on the primite of an association in the figure given (Fig. 201). Nucleus ellipsoidal, with one or two karyosomes.

Cysts spherical or subspherical, yellow in color, 60μ in diameter. Spores 8.7 by 6μ.

Taken at Roscoff, France. Host: *Machilus cylindrica* E. Geoff. Habitat: Intestine.

Schneider's figure is a paradox. It shows an association, the primite of which is a cephalont, with an epimerite. This condition is almost unique in the history of gregarines, for it is an unwritten law that only sporonts couple themselves together. I have, however, seen the phenomenon in one instance in the genus Gregarina.

GAMOCYSTIS TENAX Schneider

[Figure 201]

1875	*Gamocystis tenax*	Schneider	1875:586-7
1899	*Gamocystis tenax*	Labbé	1899:12
1913	*Gamocystis tenax*	Ellis	1913b:271

Gamocystis: Sporonts biassociative, in apposition, head to head; obese. No protomerite in the sporonts. Body ovoidal to subconical, posterior extremity rounded, nucleus spherical with one karyosome. Endocyte with large irregular granules. Cysts spherical, sporulation partial, spore ducts 15 or more in number, short, extending only into the thick transparent layer of the cyst. Spores elongate cylindrical, rounded at the ends.

Taken at Roscoff, France. Hosts: *Blattella lapponica (Ectobia lapponica* (L.) ; *Blatta lapponica).* Habitat: Intestine.

HIRMOCYSTIS GRYLLOTALPAE (Léger) Labbé

[Figure 211]

1892	*Eirmocystis gryllotalpae*	Léger	1892:112
1899	*Hirmocystis gryllotalpae*	Labbé	1899:13

Hirmocystis: Sporonts in associations of two or three. Length of sporonts 80 – 90μ. Protomerite subspherical. Cysts spherical, 60μ in diameter. Spores elongate ovoidal, 5 by 2.1μ.

Taken at Poitou, France. Host: *Gryllotalpa gryllotalpa* (L.) *(G. vulgaris)*. Habitat: Intestine.

Léger and Labbé include here, as a synonym, *Gregarina sphaerulosa* Dufour (1837:12), probably on the strength of the fact that the latter was found in the same host genus.

At the end of the chapter on Orthoptera will be found a statement that Dufour's *G. sphaerulosa* was described from cysts instead of from sporonts. Dufour did not know the mode of reproduction of the little animals he had discovered a few years previous and looked upon the white spherules as a new species. It is interesting to note that he discovered cysts from two unallied hosts and he found enough difference between the cysts to designate them as two separate species.

PILEOCEPHALUS BLABERAE (Frenzel) Labbé

[Figures 202, 203]

1892	*Gregarina blaberae*	Frenzel	1892:300-14
1899	*Pileocephalus blaberae*	Labbé	1899:20
1913	*Gregarina blaberae*	Ellis	1913b:266

Pileocephalus: Sporonts solitary, rather stout-bodied. Length of sporonts 500μ, width 150μ. Ratio length protomerite : total length sporont :: 1 : 5; width protomerite : width deutomerite : 1 1.6. Protomerite hemispherical to subglobular, 1.4 times as wide as high, very deeply constricted at septum. Deutomerite ovoidal, widest through central portion or just in front thereof, rounded at posterior end. Nucleus spherical, with one karyosome. Epimerite long, cordiform, dilated at base into a flattened sphere which is over half the width of the protomerite in its width. Epimerite equal in length to half the whole cephalont length (without the epimerite).

Cyst and spores not known.

Taken at Cordoba, Argentina. Hosts: *Blabera claraziana* Sauss. and related species. Habitat: Intestine.

Ellis replaced this species in the genus Gregarina although the only known diagnostic character, the epimerite, does not coincide with that of the genus. This structure does, however, agree in shape with that of the genus Pileocephalus according to Schneider (1875:591) and Labbé (1899:19): "Épimérite régulier simple conoide ou en fer de lance" and I have replaced it in the genus Pileocephalus.

ACTINOCEPHALUS FIMBRIATUS (Diesing) Watson

[Figures 189, 190]

1853	*Gregarina Locustae Carolinae*	Leidy	1853:239
1856	*Gregarina Locustae carolinae*	Leidy	1856:47
1859	*Gregarina fimbriata*	Diesing	1859:730
1903	*Stephanophora locustaecarolinae*	Crawley	1903:54
1907	*Stephanophora pachyderma*	Crawley	1907:226
1913	*Actinocephalus pachydermus*	Ellis	1913b:278
1916	*Actinocephalus fimbriatus*	Watson	(This paper)

Actinocephalus: Sporonts solitary, obovate. Maximum length of sporonts 500μ. Protomerite hemispherical, not constricted at septum but contour continuous with that of deutomerite. Latter tapers slightly, ending in a blunt point. Sarcocyte very thick, especially over anterior end of protomerite. Endocyte black in deutomerite, less dense in protomerite. Nucleus spherical with 12 or more small karyosomes. Epimerite an inverted campanula, sessile, with ten or more slender digitiform processes directed upward along the periphery.

Cysts and spores unknown.

Taken at Wyncote, Pa. Host: *Dissosteira carolina* (L.); Habitat: Intestine.

A cephalont of this species was first seen by Leidy in 1853. He described it and the sporonts of *Gregarina locustae carolinae* together under the latter name.

In 1903, Crawley renamed the species *Stephanophora locustaecarolinae* from the character of the epimerite, as drawn by Leidy. Crawley did not see the species then. The error of inclusion was discovered by Crawley from new material in 1907, and he then separated the two species, describing each in detail. The former he called *Stephanophora pachyderma,* the latter by the original name.

The first binomial name given to this species, however, was *Gregarina fimbriata,* which Diesing used. He redescribed *Gregarina locustae carolinae* of Leidy under a new name adding no new material. He says of this species "proboscis digitato-fribriato", which definitely places his description.

Ellis transferred the species in question to the genus Actinocephalus, where it belongs because of the character of the epimerite. The genus Stephanophora was distinguished by its flat cushion-like epimerite with stout broad digits rising from the periphery. The genus has now been merged with another and the name discontinued.

INDETERMINATE SPECIES

GREGARINA CONICA Dufour

[Figure 102]

1837	*Gregarina conica*	Dufour	1837:12
1851	*Gregarina conica*	Diesing	1851:8
1863	*Gregarina conica*	Lankester	1863:95

Dufour's description is as follows:

"Oblongo-conica; cephalothorace subgloboso abdominis tertiam partem adaequante. Hab. Coleopterorum et Gryllorum."

In 1826 Dufour described an intestinal parasite from Coleoptera. In 1828 he named it Conica; in 1837 he gave as hosts the above animals and named the parasite *Gregarina conica.* The parasite is illustrated in his 1837 paper. That he had two species under consideration is obvious from his drawings as seen in Figures 101 and 102, one being labelled as from Coleoptera and the other from Gryllus. The former has a crenulate, stalked epimerite, the latter a simple spherical stalked one. The former figure has been homologized with several drawings by subsequent writers and represented the parasite described in the chapter on Coleopteran parasites under the name of *Actinocephalus conicus* (Dufour) Stein.

Stein described a parasite, *Actinocephalus lucani,* from a beetle, which is identical with Dufour's drawing 7. He did not know of Dufour's paper and the previous discovery of the species, but Frantzius (1848:195) did, and mentioned Stein's *Actinocephalus lucani* from Lucanus, leaving the original *Gregarina conica* Dufour from Gryllus only.

Diesing (1851) listed both *G. conica* Dufour from Coleoptera and Gryllus, and *G. Lucani* Stein from *Lucanus parallelopipedus.*

Lankester did likewise. After his citation, *G. conica* dropped out of the literature. It is obvious that Dufour found a parasite in Orthoptera, but what it was no one can say. He did not find associations and no one knows whether he saw only the isolated cephalonts with the epi-

merites, which he shows in his drawing, or whether he saw sporonts which were not associative.

So the generic position of the species is doubtful. The family determination is fairly definite, from the simple spherical epimerite, but the species must be relegated to the group of the indeterminate species.

GREGARINA DAVINI Léger and Duboscq

[Figure 204]

1899 *Gregarina Davini* Léger and Duboscq 1899:xxxviii-xl

Gregarina: Sporonts not described, cephalonts alone known. Nucleus spherical, with a large irregularly shaped karyosome. Epimerite large and spherical, set upon a rather long stout collar formed by a projection of the anterior end of the protomerite.

Cysts spherical, with 12 or more long spore ducts from which spores are extruded in chains. Spores barrel shaped, 8μ long.

Taken at Marseilles, France. Host: *Gryllomorpha dalmatina* Ocsk. Habitat: Intestine and caecum.

Although sporonts have not been found, the species is undoubtedly a member of the genus Gregarina from the mode of dehiscence and the shape of the epimerite. It cannot be determined whether or not the species has been described elsewhere from the sporont in addition to these other factors under a different name. Until sporonts are found and correlated with the description herewith, the species must remain incomplete.

MISCELLANEOUS

GREGARINA SPHAERULOSA Dufour

[Figure 179]

1837	*Gregarina sphaerulosa*	Dufour	1837:12
1851	*Gregarina sphaerulosa*	Diesing	1851:11
1863	*Gregarina sphaerulosa*	Lankester	1863:94
1899	*Hirmocystis gryllotalpae*	Labbé	1899:13

Dufour described this form as follows:

"Subspherica alba, cephalothorace abdomen adaequanta. Hab. in ventriculo Oedipodarum et Gryllotalpae.

Elle–est – – – egàlant à peine la grosseur d'une tête de fine épingle a insectes; – – –. Les individus bien adultes semblent résulter de l'union de deux hémisphères. Des yeux peu rigoreux pourraient croire que ce sont deux individus accouplés bout à bout."

It is obvious from the description and from the figure that what Dufour

saw and named were not sporonts but cysts formed by the union of two equal or sub-equal sporonts. None of his other descriptions of sporonts applies to the particular species of Orthoptera from which these cysts were taken, so no sporonts, but only cysts, must have been present in the host. Dufour did not, as might have been the case, describe the cysts and sporonts in the same host as separate species. These cysts were taken from *Oedipoda coerulescens* and from *Gryllotalpa* sp.

Neither Frantzius nor Lankester mentioned the 'species' and the host. Labbé mentioned it as a synonym of *Hirmocystis gryllotalpae* (Léger) Labbé, probably from an identity of host genera and certainly not because of any similarity in appearance.

GREGARINA SOROR Dufour

[Figure 180]

1837	*Gregarina soror*	Dufour	1837:12
1851	*Gregarina soror*	Diesing	1851:11
1863	*Gregarina soror*	Lankester	1863:94
1899	*Gregarina soror*	Labbé	1899:34

Just as in the instance above, Dufour has here described cysts instead of sporonts. His words are as follows:

"Subsphericum alba, cephalothorace abdominis dimidiam partem adaequante."

"Celle-ci n'est peut-être qu'une variété de la précédente; mais le cephalothorace ne forme pas, comme dans cetta dernière, la moite de tout le corps."

The cyst in question consists of two unequal parts, making the "cephalothora" less than half the sphere.

Diesing and Lankester mention the form and Labbé places it in his "Uncertain" group under the original name.

POLYCISTID GREGARINES IN THE COLEOPTERA*

NAME OF PARASITE	NAME OF HOST
DIDYMOPHYIDAE	
Didymophyes gigantea Stein	*Oryctes* sp. larva.
	Oryctes nasicornis (L.) larva.
	Phyllognathus sp. larva.
Didymophyes paradoxa Stein	*Geotrupes stercorarius* (L.)
Didymophyes leuckarti Marshall	*Aphodius prodromus* (Brahm.)
	Aphodius nitidulus F.
Didymophyes minuta (Ishii) Watson	*Tribolium ferrugineum* F.
ACTINOCEPHALIDAE	
Actinocephalus concius (Dufour) Frantzius	*Dorcus parallelopipedus* (L.)
Actinocephalus dytiscorum (Frantzius) Watson	*Dytiscus marginalis* L. larva.
Actinocephalus stelliformis Schneider	*Ocypus olens* Mull. larv. and ad.
	Carabus auratus L.
	C. violaceus L.
	Rhizotrogus sp. larva.
Actinocephalus digitatus Schneider	*Chlaenius vestitus* (Payk.)
Actinocephalus acutispora Léger	*Silpha laevigata* F.
Actinocephalus americanus Crawley	*Galerita bicolor* Drury
Actinocephalus harpali (Crawley)	*Harpalus caliginosus* Fab.
Actinocephalus dicaeli (Crawley) Ellis	*Dicaelus ovalis*
Actinocephalus crassus (Ellis)	*Leptochirus edax* Sharp
Actinocephalus zophus (Ellis)	*Nyctobates barbata* Knoch
	Alobates pennsylvanica deGeer
Actinocephalus gimbeli (Ellis) Watson	*Harpalus pennsylvanicus* Dej.
Asterophora philica (Leidy) Crawley	*Nyctobates pennsylvanica* de-Geer
Asterophora cratoparis Crawley	*Cratoparis lunatus* Fab.
Beloides firmus (Léger) Labbé	*Dermestes lardarius* L. larva
Beloides tenuis (Léger) Labbé	*Dermestes undulatus* Brahm. larva
Bothriopsis histrio Schneider	*Colymbetes fuscus* L.
	Hydaticus cinereus L. larva
	Acilius sulcatus L.
	Dytiscus sp. larva

*The species are arranged in families, the families include genera in alphabetical order, and under each genus the species are placed in chronological sequence.

Bothriopsis terpsichorella (Ellis) Watson	*Hydrophilus* sp.
Legeria agilis (Schneider) Labbé	*Colymbetes* sp. larva
Phialoides ornata (Léger) Labbé	*Hydrophilus piceus* (L.) larva
Pileocephalus bergi (Frenzel) Labbé	*Necrobia ruficollis* Fabr.
Pyxinia rubecula Hammerschmidt	*Dermestes lardarius* L. larva
	D. vulpinus F. adult
Pyxinia crystalligera Frenzel	*Dermestes vulpinus* Fabr. larva
	D. peruvianus Casteln. larva, ad.
Pyxinia frenzeli Laveran and Mesnil	*Attagenus pellio* L.
Pyxinia möbuszi Léger and Duboscq	*Anthrenus verbasci* Olivier, larva
Stictospora provincialis Léger	*Melolontha* sp. larva
	Rhizotrogus sp. larva
Steinina ovalis (Stein) Léger and Duboscq	*Tenebrio molitor* L. larva
Steinina obconica Ishii	*Tribolium ferrugineum* F.
Steinina rotunda Watson	*Amara angustata* Say
Steinina harpali Watson	*Harpalus pennsylvanicus longior* (Kirby)
Stylocystis ensifera (Ellis)	*Leptochirus edax* Sharp

STYLOCEPHALIDAE

Cystocephalus algerianus Schneider	*Pimelia* sp.
Lophocephalus insignis (Schneider) Labbé	*Helops striatus* Geoff.
Oocephalus hispanus Schneider	*Morica* sp.
Stylocephalus oblongatus (Hammerschmidt) Watson	*Opatrum sabulosum* (L.)
	Asida grisea (F.)
Stylocephalus longicollis (Stein) Watson	*Blaps mortisaga* L.
Stylocephalus brevirostris (Kölliker) Watson	*Hydrophilus* sp. larva
Stylocephalus gladiator (Blanchard) Watson	*Helenophorus collaris* L.
Stylocephalus giganteus Ellis	*Eleodes* sp.
	Asida sp.
	Asida opaca Say
	Eusattus sp.
Sphaerorhynchus ophioides (Schneider) Labbé	*Acis* sp.

ACANTHOSPORIDAE

Acanthospora pileata Léger	*Omoplus* sp. larva
	Cistelides sp.
Acanthospora polymorpha Léger	*Hydrous caraboides* (L.) larva
Ancyrophora gracilis Léger	*Carabus* sp. larva and ad.
	Carabus auratus L.
	Carabus violaceus L. larva and ad.
	Silpha thoracica L. larva
Ancyrophora uncinata Léger	*Dytiscus* sp.
	Colymbetes sp.
	Sericostoma sp.
	Limnophilus rhombicus (L.)
Cometoides capitatus (Léger) Labbé	*Hydrous* sp. larva.
Cometoides crinitus (Léger) Labbe	*Hydrobius* sp. larva
Corycella armata Léger	*Gyrinus natator* (L.) larva

GREGARINIDAE

Hyalospora roscoviana Schneider	*Petrobius maritimus*
Sphaerocystis simplex Léger	*Cyphon pallidulus* Boh.
Euspora fallax Schneider	*Rhizotrogus aestivus* Oliv.
Hirmocystis asidae Léger	*Asida servillei* Sol.
Hirmocystis harpali Watson	*Harpalus pennsylvanicus erythropus* (Dej.)
Gregarina cuneata Stein	*Tenebrio molitor* L. larva and ad.
Gregarina polymorpha (Hammerschmidt) Stein	*Tenebrio molitor* L. larva and ad.
Gregarina amarae Frantzius	*Poecilus cupreus* (L.)
Gregarina tenuis Hammerschmidt	*Allecula* sp.
Gregarina elongata Frantzius	*Crypticus* sp.
Gregarina scarabaei Lankester	*Scarabaeus relictus* larva
Gregarina passali Lankester	*Passalus cornutus* Fab.
Gregarina melolonthae Lankester	*Melolontha brunnea*
Gregarina munieri (Schneider) Labbé	*Timarcha tenebricosa* (F.)
	Chrysomela violacea (Goeze)
	C. haemoptera L.
Gregarina laucournetensis (Schneider) Labbé	*Parnus* sp.
Gregarina statirae Frenzel	*Statira unicolor* Blanch.
Gregarina longirostris (Léger) Labbé	*Thanasimus formicarius* (L.)

Gregarina acuta (Léger) Labbé	*Trox perlatus* Scriba
Gregarina steini Berndt	*Tenebrio molitor* L. larva
Gregarina parva (Crawley) Watson	*Harpalus pennsylvanicus* Dej.
	H. caliginosus Fab.
Gregarina lucani (Crawley) Watson	*Lucanus dama* Thunb.
Gregarina cavalierina Blanchard	*Dendarus tristis* Rossi (=*coarcticollis* Mls.)
Gregarina socialis Léger	*Eryx ater* Fabr. larva
Gregarina guatemalensis Ellis	*Ninus interstitialis* Esch.
Gregarina grisea Ellis	*Tenebrio castaneus* Knoch
Gregarina minuta Ishii	*Tribolium ferrugineum* F.
Gregarina katherina Watson	*Coccinella novemnotata* Herbst.
Gregarina barbarara Watson	*Coccinella* sp.
Gregarina fragilis Watson	*Coccinella* sp.
Gregarina tenebrionella Watson	Tenebrionidae larva
Gregarina gracilis Watson	Elateridae larva
Gregarina intestinalis Watson	*Pterostichus stygicus* Say
Gregarina monarchia Watson	*Pterostichus stygicus* Say
Gregarina globosa Watson	*Coptotomus interrogatus* (Fab.)
Gregarina platyni Watson	*Platynus ruficollis* Marsh.

UNCERTAIN SPECIES IN GENUS GREGARINA

Gregarina elaterae Crawley	*Elater* sp. larva
Gregarina curvata (Frantzius) Diesing	*Cetonia aurata* larva

UNCERTAIN SPECIES IN UNCERTAIN FAMILIES

Gregarina boletophagi Crawley	*Boletophagus cornutus*
Gregarina microcephala Leidy	*Arrhenoplita bicornis* Olivier
Gregarina ovalis (Crawley) Watson	Cucujidae larva
Gregarina coptotomi Watson	*Coptotomus interrogatus* Fab.
Stylocephalus sp.	*Xylopinus saperdioides* Oliv.
Gregarina sp. Crawley	Host not given

DIDYMOPHYES GIGANTEA Stein

[Figures 61, 63]

1848	*Didymophyes gigantea*	Stein	1848:186
1863	*Gregarina gigantea*	Lankester	1863:95
1889	*Didymophyes gigantea*	Mingazzini	1889:234-9
1892	*Didymophyes gigantea*	Léger	1892:106

Didymophyes: Sporonts biassociative, slender, very much attenuated. Average length 1 cm., average width 80 to 100μ. Ratio length protomerite : total length primite :: 1 : 30 to 1 : 40; width protomerite : width deutomerite :: 1 : 0.66 to 1 : 1. Protomerite dome shaped with a short wide neck just anterior to septum. Deutomerites two in number, cylindrical, widest at septum and tapering gradually, ending in a blunt rounded extremity.* Septa convex upward. Deutomerites nearly equal in length. Nuclei not visible in vivo and not described. Endocyte dense, deeply staining. Epimerite a cylindrical-conical papilla.

Cysts spherical, 600 to 700μ in diameter. Spores ovoidal, two integuments, 6 by 6.5μ.

Taken at Berlin, Naples, and Poitiers. Hosts: Larvae of *Oryctes nasicornis* (L); of *Phyllognathus* sp. and of *Oryctes* sp. Habitat: Intestine.

DIDYMOPHYES PARADOXA Stein

[Figures 62, 72]

1848	*Didymophyes paradoxa*	Stein	1848:223
1863	*Gregarina paradoxa*	Lankester	1863:95
1892	*Didymophyes rara*	Léger	1892:106
1899	*Didymophyes paradoxa*	Labbé	1899:8

Didymophyes: Sporonts biassociative, short. Length and width not given. Ratio length protomerite : total length :: 1 : 7 to 1 : 9; width protomerite : width deutomerite :: 1 : 1 to 1.1 : 1. Protomerite dome shaped, considerably flattened, twice as wide as high, a little wider than deutomerite. First deutomerite cylindrical, of same length or 1½ times longer than second; second tapering to a blunt point. Septa con-

*Stein's figure indicates that the first deutomerite in its anterior third is narrower than at the first septum, becoming as wide at the septum between the two deutomerites as it is at the septum between protomerite and the first deutomerite. This width is retained throughout the second deutomerite.

vex upward. Nuclei visible, spherical and large, one in each deutomerite. Cyst and spores unknown.

Taken at Berlin and Poitiers. Hosts: *Geotrupes* sp. and *Geotrupes stercorarius* (L.). Habitat: Intestine.

DIDYMOPHYES LEUCKARTI Marshall

[Figures 59, 60]

1893	*Didymophyes leuckarti*	Marshall	1893:41-2

Didymophyes: Sporonts bi- or tri- associative. Length 280 to 1120μ. Width not given. Ratio length protomerite : total length :: 1 : 4 in the association of two; 1 : 11 in the triple association. Ratio width protomerite : width deutomerite :: 1 : 1.3 to 1 : 5. Protomerite dome shaped, broadly rounded, twice as wide as high, constriction at septum. Either 2 or 3 deutomerites, attached one behind the other, each nucleated and separated from others by a straight septum and a conspicuous constriction. Deutomerites barrel shaped, but little wider than protomerite, last one tapering and ending in a more or less broadly rounded extremity. Endocyte dense in both protomerite and deutomerite. Nuclei spherical, containing many small chromatin bodies.

Cysts spherical, one long spore duct. Spores not known. Hosts: *Aphodius prodromus* (Brahm.) and *A. nitidulus* F. Habitat : Intestine.

The cyst dehiscence as seen by Marshall does not coincide with that reported by Léger. The latter mentions simple rupture; the former dehiscence by one long spore duct. If the methods described by both authors are to be accepted, various species in the same genus must have different modes of dehiscence.

DIDYMOPHYES MINUTA (Ishii) Watson

[Figure 71]

1914	*Gregarina minuta*	Ishii	1914:436-7
1916	*Didymophyes minuta*	Watson	(This paper)

Didymophyes: Sporonts elongate. Length 188μ, width 26μ. Ratio length protomerite : total length :: 1 : 23; width protomerite : width deutomerite :: 1 : 1.5. Protomerite flattened somewhat, twice as wide as high, deep constriction at septum. Deutomerites cylindrical, about equal in length, constriction between the two, posterior end broadly

rounded. Nuclei spherical, one large karyosome in each. Endoplasm not dense.

Cyst and spores unknown.

Taken in the Province of Izu, Japan. Host: *Tribolium ferrugineum* F. Habitat: Intestine.

Under the name *Gregarina minuta,* Ishii described and illustrated two species of gregarines, one proving to be the above member of the family Didymophyidae, the other a true Gregarina. The two forms were shown to be different by the absence of a protomerite in the satellite in the former and its presence in the latter. There was also a difference in the size of the two kinds of associations. The smaller were those of a true Gregarina, having a protomerite in the satellite, and the name used by the author, *Gregarina minuta,* applies to them only. The larger associations are those of the other form, and I have called this species *Didymophyes minuta* (Ishii). For a more detailed argument concerning these species, see appendix at the end of this chapter.

ACTINOCEPHALUS CONICUS (Dufour) Frantzius

[Figures 75, 76, 101, 102, 103]

1826	sp.	Dufour	1826:43
1828	– – *Conica*	Dufour	1828:367
1837	*Gregarina conica*	Dufour	1837:12
1848	*Actinocephalus Lucani*	Stein	1848:223
1848	*Actinocephalus Lucanus*	Frantzius	1848:195
1848	*Actinocephalus conicus*	Frantzius	1848:195
1851	*Gregarina Lucani*	Diesing	1851:14
1851	*Gregarina conica*	Diesing	1851:8
1863	*Gregarina Lucani*	Lankester	1863:95
1863	*Gregarina conica*	Lankester	1863:95
1892	*Stephanophora radiosa*	Léger	1892:127
1899	*Stephanophora lucani*	Labbé	1899:23
1913	*Actinocephalus lucani*	Ellis	1913b:277

Actinocephalus: Sporonts solitary, length 300 to 400μ. Width not given. Ratio length protomerite : total length :: 1 : 5 (without epimerite); width protomerite : width deutomerite :: 1 : 3. Protomerite nearly globular, carrying at the apex a persisting epimerite, situated upon a thick prominent neck. Epimerite larger than protomerite, consisting of hemispherical plateau around the periphery of which is situated a corona of 12 or more large upwardly directed digitiform processes. Deep constriction at septum. Deutomerite widest above middle,

tapering but ending in a blunt, rounded extremity. Nucleus spherical with several karyosomes or a band of chromidial bodies. Endocyte yellowish.

Cysts spherical, 250μ in diameter. Spores long, cylindrical, biconical at ends, 13.5 by 4.5μ.

Taken at Berlin and at Tourraine (France). Host: *Dorcus parallelopipedus* (L.) *(Lucanus p.* Fabricus). Habitat: Intestine.

There was considerable confusion regarding this species more than half a century ago. Dufour (1826:43) said:

"Dans le tube alimentaire de divers Coleoptéres, notamment du *Lucanus parallelopipedus,* de plusieurs Melasomes et de la *Timarcha tenebricosa,* j'ai trouve abondamment une espéce de Vers intestineaux, dont je joins ici le dessin."

It is interesting to note that he called the gregarine an intestinal worm. Two years later he added:

"L'espèce que j'ai dit habiter les entrailles de divers Coleoptéres, merite, à cause de sa forme, le nom Conica."

By this time Dufour was evidently including many species of gregarines under the same name, not differentiating them from one another.

In 1837, he described in detail, covering two pages, a new genus he established to include a half dozen species which he had discovered, and called the genus Gregarina. One of the species enumerated is *Gregarina conica* and its hosts are given as Coleoptera and Gryllus. That at least two species were concerned in this inclusion is indicated by his figures 7 and 7a, Pl. I, copied in my figures 101 and 102. The figures are similar in one respect, they are both conical at the posterior ends. The protomerites, however, are very unlike. Figure 101 compares favorably, despite its fanciful epimerite, with Stein's figure 35, Pl. IX (1848), my figure 75, from the intestine of the same beetle. These two species are probably the same and the name of the species should thus be *Actinocephalus conicus* (Dufour) Frantzius, Dufour having first named the species and Frantzius having placed it properly.*

Frantzius (1848) recorded both *Actinocephalus conicus* Dufour and *A. Lucanus* Stein and he mentioned as host of the former Gryllus, and of the latter Lucanus.

Diesing recorded *Gregarina conica* Dufour from "Coleopterorum et Gryllorum ventriculus (Dufour)" and *G. lucani* Stein from *Lucanus parallelopipedus.*

Lankester listed both species. Léger (1892) described the species as a new one under the name *Stephanophora radiosa.* His description

*Dufour's Figure 7a is placed in the chapter on Orthopteran Parasites, under the heading Indeterminate Species, *G. conica* Duf.

of the new genus Stephanophora does not differ from Stein's genus Actinocephalus. Léger's words are as follows:

"Appareil de fixation – – constituté par un plateau epais bordé d'une couronne de tentacules globuleux.

Grégarines toujours solitaires, fixeés pendant la plus grande partie de leur existence; – – –.

Kystes spheriques dehiscents par simple rupture – – –. Spores cylindro-biconiques."

Stein's diagnosis of the genus is as follows:

Die andre Form des Haftapparates ensteht dadurch, dass sich der Kopf nach vorn in einen kurzen Stiel verengert, der sich in eine flache, runde, am Rande gekerbte, auf dem Stiel senkrecht stehende Schiebe erweitert. [My Fig. 75]. Die vordere, zum Anheften dienende Fläche der Schiebe ist in der Mitte in einer, dem Durchmesser des Stiels gleichkommenden Ausdehnung glatt, von diesem glatten Centrum aus aber bis zur Peripherie sehr regelmässig strahlenförmig in Falten gelegt. Jede Einfaltungsfurche fällt einer Einkerbung des Seheibenrandes zusammen. Ich vereinige die mit einem solchem Haftapparat versehenen Formen zu der Gattung Actinocephalus."

The two descriptions are thus synonymous and but one species is involved, as well as but one genus, the epimerite being stalked, with digitiform processes radiating from a flat central plate. In Stein's drawing the processes turn backwards, in Léger's they point directly forward, but this is of no import.

Labbé saw the error in considering the two species distinct. He united them under the species name given by Stein, leaving the species in the genus of Léger, calling the form *Stephanophora lucani* (Stein). Ellis replaced the species in the genus to which it was assigned by Stein. But, according to priority, and from the exhibition of all the evidence in the case, the species name given by Dufour should stand valid and the species be called *Actinocephalus conicus* (Dufour) Frantzius.

The removal of the species from the genus Stephanophora takes from the genus the type and only species and the genus thus drops out of usage.

ACTINOCEPHALUS DYTISCORUM (Frantzius) Watson

[Figure 148]

1848	*Sporadina Dytiscorum*	Frantzius	1848:195
1851	*Gregarina Dytiscorum*	Diesing	1851:12
1863	*Gregarina Dytiscorum*	Lankester	1863:94
1890	*Ancyrophora uncinata*	Labbé	1899:28-9
1916	*Actinocephalus dytiscorum*	Watson	(This paper)

Actinocephalus: Sporonts robust. Ratio length protomerite : total length :: 1 : 7; width protomerite : width deutomerite :: 1 : 1. Protomerite broad and low, twice as wide as high, flattened in front. Very slight constriction at septum. Deutomerite at septum same width as protomerite in front in septum, retaining same width throughout anterior half. Posterior half much narrower, tapering to a blunt point. Cysts large, spherical, spores not known.

Taken at ———, Germany. Host: *Dytiscus* sp. Habitat: Intestine.

This species is known from the drawings of Frantzius, one being of an adult sporont (?) and the other of a cyst. Diesing gives as host *Dytiscus marginalis* larva. Labbé regards the species as synonymous with *Ancyrophora uncinata* Léger, from a similarity of the host, *Dytiscus*.

The sporont, however, has no resemblance to that of Léger's species, and, although the epimerite of the species in question is not known, it seems to have an individuality.

ACTINOCEPHALUS STELLIFORMIS Schneider

[Figures 67, 69, 73]

1875	*Actinocephalus stelliformis*	Schneider	1875:588-9
1893	*Actinocephalus stelliformis*	Pfeiffer	1893:5-11

Actinocephalus: Dimensions not given. Ratio length protomerite : total length :: 1 : 4.5 to 1 : 8; width protomerite : width deutomerite :: 1 : 1.4. Protomerite cylindrical, surmounted by a broadly rounded anterior extremity; same width throughout posterior half, width equal to length. Constriction at septum. Epimerite persisting, a small globular structure surmounted by a corona of recurved processes, each slender at the base, dilated and bifid at the distal extremity. Deutomerite widest above the middle, tapering to a long,

sharply pointed extremity. Endocyte very dense. Nucleus small, spherical. Cyst and spores unknown.

Taken at Paris. Hosts: *Ocypus olens* (Mull.) *(Staphylinus o.)* larva and adult; *Carabus auratus* L.; *Carabus violaceus* L.; and *Rhizotrogus* sp. lv. Habitat: Intestine.

Schneider mentions three varieties of this species: a) body regularly lanceolate, epimerite persistent; b) body subspherical; c) body extremely elongate. Pfeiffer found the species in *Carabus violaceus* L.

ACTINOCEPHALUS DIGITATUS Schneider

[Figure 66]

1875 *Actinocephalus digitatus* Schneider 1875:590

Actinocephalus: Sporonts solitary, short, obese. Measurements not given. Ratio length protomerite : total length :: 1 : 4.5. Ratio width protomerite : width deutomerite :: 1 : 1.4. Protomerite dome-shaped, widest in posterior half, width equal to height. Constriction at septum. Deutomerite rather short, widest a short distance below septum and tapering gradually to a sharp point. Nucleus small, spherical. Epimerite persistent, a globular structure surmounted by a rosette of 8 to 10 recurved digitiform processes rounded at their extremities. Cysts and spores unknown.

Taken at Paris. Host: *Chlaenius vestitus* (Payk.). Habitat: Intestine.

Schneider says:

"L'Actinocephalus Lucanus de Stein, provenant de la larva d'un *Lucanus parallelopipedus,* est une espèce fort voisine de celle-ci."

ACTINOCEPHALUS ACUTISPORA Léger

[Figures 212, 213]

1892 *Actinocephalus acutispora* Léger 1892:142
1899 *Actinocephalus acutispora* Labbé 1899:26

Actinocephalus: Sporonts solitary, length 1000 to 1500μ. Width not given. Ratio length protomerite : total length :: 1 : 11; ratio width protomerite : width deutomerite :: 1 : 1.4. Protomerite 1.5 times as long as wide, cylindrical, rounded at the top and slightly dilated in posterior fourth. Constriction at septum. Deutomerite very long and

slender, slightly wider than protomerite at shoulder and tapering to a long acutely pointed posterior extremity. Epimerite a spherical button situated upon a short collar and consisting of 12 slender incurved processes terminating in obtuse points. Endocyte brownish yellow. Nucleus spherical, containing 3 to 7 karyosomes.

Cysts ovoidal, 550 to 600μ by 280μ. Dehiscence by simple rupture. Spores obese, acutely pointed, two sizes, 4.5 by 2.8μ and 6.4 by 3.6μ.

Taken at Poitiers, France. Host: *Silpha laevigata* F. Habitat: Intestine.

ACTINOCEPHALUS AMERICANUS Crawley

[Figure 64]

1903	*Actinocephalus americanus*	Crawley	1903a:636

Actinocephalus: The generic determination of this species is not absolute. Crawley's description is quoted below:

"This species is created for a single individual found in *Galerita bicolor* Drury. – – – . It is placed in the genus Actinocephalus on account of the form of both protomerite and deutomerite, the presence of several karyosomes in the nucleus and the fact that the host was a carnivorous Arthropod. The gregarine was 200μ long, 35μ of which represented the length of the protomerite, 45μ broad. The epicyte – – showed a little papilla at the anterior tip of the protomerite. – – The endocyte was much denser in the deutomerite than in the protomerite. – – –."

It is probable that Crawley's determination is correct but the recovery of cysts and spores as well as the epimerite is needed to substantiate the determination.

ACTINOCEPHALUS HARPALI (Crawley)

[Figure 70]

1903	*Gregarina harpali*	Crawley	1903:49
1903	*Actinocephalus harpali*	Crawley	1903a:637-8

Actinocephalus: Sporonts solitary, obese. Length 225 to 1200μ. Width not given. Ratio length protomerite : total length :: 1 : 6.5; width protomerite : width deutomerite :: 1 : 1.2. Protomerite broadly dome-shaped, twice as wide as high, flattened at the free end, deeply constricted at the septum. Deutomerite widest a short distance below septum where it is but little wider than the protomerite, tapering from anterior fourth to a blunt posterior end. Endocyte very dense, blackish,

of equal density in protomerite and deutomerite. Nucleus large, spherical, containing several karyosomes.

Cysts spherical, 640μ in diameter, dehiscing by simple rupture. Spores 9 by 7.5μ, diamond shaped.

Taken at Wyncote, Pa. Host: *Harpalus caliginosus* Fab. Habitat: Intestine.

"These gregarines were present in the intestine of the one beetle examined in hundreds."

ACTINOCEPHALUS DICAELI (Crawley) Watson

[Figure 100]

1903	*Gregarina discaeli*	Crawley	1903:47
1903	*Gregarina dicaeli*	Crawley	1903a:641
1913	*Actinocephalus discaeli*	Ellis	1913b:279
1916	*Actinocephalus dicaeli*	Watson	(This paper)

Actinocephalus: Sporonts solitary, greatly elongate. Length 1200μ. Ratio length protomerite : total length :: 1 : 15; width protomerite : width deutomerite :: 1 : 1.2. Protomerite pentagonal, seen in lateral optical section, widest through middle, flattened on top, width about equal to height. Slight constriction at septum. Deutomerite very elongate, cylindrical, slightly tapering to a blunt point. Epimerite not known. Endocyte dense, opaque in deutomerite, nearly transparent in protomerite. Nucleus spherical, with several karyosomes. Cyst and spores not known.

Taken in Pennsylvania. Host: *Dicaelus ovalis* Lec. Habitat: Intestine.

Crawley placed this species in the genus Gregarina, with a question. In his later paper (1903a) he left it in the same genus but in a list of eight doubtful species.

"This gregarine is placed in the genus Actinocephalus because of the general shape of the sporont and the coleopteran host; it was removed from the genus Gregarina because the sporonts do not form associations."

Its generic position is still doubtful and from the data at hand might belong to any of these families: Actinocephalidae, Stylocephalidae or Acanthocephalidae.

The generic name of the host and the specific name of the parasite were both misspelled by Crawley in his original paper. This error was corrected in his second memoir; but Ellis copied the original error, overlooking Crawley's careful explanation of the misprint.

ACTINOCEPHALUS CRASSUS (Ellis)

[Figure 68]

1912	*Stephanophora crassa*	Ellis	1912a:688-9
1913	*Actinocephalus crassus*	Ellis	1913b:278

Actinocephalus: Sporonts solitary, obese. Length 50 to 60μ; width not given. Ratio length protomerite : total length :: 1 : 3.3 to 1 : 3.5. Width protomerite : width deutomerite :: 1 : 1 to 1 : 5. Protomerite dome shaped, a little wider than high, constricted at septum. Deutomerite widest in anterior third, where it is a little wider than the protomerite, narrowing abruptly to a rather sharply pointed posterior extremity. Nucleus small, spherical. Cyst and spores not known.

Taken at Quirigua, Guatemala. Host: *Leptochirus edax* Sharp. Habitat: Intestine.

The determination of the species above is not absolute. Since generic diagnoses depend on the character of the epimerite and the spores as well as on other factors, the absence of these factors tends to make the determination indeterminate. By elimination of negative factors, however, the generic determination is probably correct.

ACTINOCEPHALUS ZOPHUS (Ellis)

[Figure 74]

1913	*Stephanophora zopha*	Ellis	1913a:201-2
1913	*Actinocephalus zophus*	Ellis	1913b:278

Actinocephalus; Sporonts elongate, length 1200 to 1600μ. Width not given. Ratio length protomerite : total length :: 1 : 8 to 1 : 13; width protomerite : width deutomerite :: 1 : 1.7. Protomerite globose, rounded in front. Constriction at septum. Width same as length. Deutomerite slender, elongate. Widest at shoulder, cylindrical, tapering at posterior end to a sharp point. Epimerite persistent, constriction at base and terminating in a corona of 9 or more small regular, rounded, digitiform processes. Endocyte brown, nucleus not seen. Cyst and spores not known.

Taken at New Orleans, La., and at East Falls Church, Va. Hosts: *Nyctobates barbata* Knoch *(N. barbarata* Kn.); *Nyctobates pennsylvanica* deGeer. Habitat: Intestine.

This species was described by Ellis as belonging to the genus

Stephanophora; an error he afterwards corrected and placed the species in the present genus.

Ellis mentions the fact that the record of a species found by Crawley among Leidy's manuscripts seems to indicate that the latter is the same species as that which he describes as *A. zophus.* His words are as follows:

> "Figs. 29 and 30 (Crawley 1903, Pl. III), as taken from Leidy's Mss. are of different Gregarines, a fact recognized by Crawley. Fig. 30 represents a gregarine closely related to *G. grisea,* while Fig. 29 is apparently of a sporont of *S. zopha.*"

A comparison of *S. zopha* (Fig. 74 of this paper) and of Leidy's drawing (Fig. 65 of this paper) will indicate that there is a difference in the shape of the sporonts. The protomerite of Leidy's species is wider than the deutomerite; in Ellis', narrower. In the former it is flattened, in the latter elongated. The deutomerite in the former tapers from the septum to a long, sharply pointed posterior extremity. In *S. zopha* the deutomerite is widest at the shoulder, a little below the septum and is cylindrical for two-thirds of its length, ending in a slightly tapering, bluntly pointed cone. From these facts and because the epimerite of Leidy's species was not seen, I am inclined to think the two species are not identical and that the one in Leidy's drawing should be relegated to the list of indeterminate species. (See list of such species at end of this chapter).

ACTINOCEPHALUS GIMBELI (Ellis) Watson

[Figures 126, 127]

1913	*Stenophora gimbeli*	Ellis	1913:464
1916	*Actinocephalus gimbeli*	Watson	(This paper)

Actinocephalus: Sporonts solitary, obese. Length 520μ. Width not given. Ratio length protomerite : total length :: 1 : 5 to 1 : 6. Ratio width protomerite : width deutomerite :: 1 : 2. Protomerite broadly rounded in front, widest in middle portion, twice as wide as high. Conspicuous constriction at septum. Deutomerite ovoidal, widest through middle, tapering and ending in a bluntly pointed posterior extremity. Endocyte very dense, black in deutomerite, lighter in protomerite, but dense in anterior end. Nucleus not seen. Cyst and spores not known.

Taken at Vincennes, Indiana. Host: *Harpalus pennsylvanicus* Dej. Habitat: Intestine.

Ellis described this species as a Stenophora because of

"– – the papilla at the anterior end, which results from the expansion of the thin epicyte. Such a process has already been described by the writer (1912:681-6) in another species of this genus, *S. cockerellae* Ellis, from Guatemala."

The shape of the protomerite is very unlike that of the Stenophoridae, being twice as wide as high, while in this family it is globular or subglobular. The Stenophoridae are confined to the Diplopoda. Although no positive factors are present to indicate its position, yet from exclusion of factors, this species would fall under the family Actinocephalidae. The general shape is not unlike that of *Actinocephalus conicus* (Dufour) Stein (Figs. 75 and 76). The two most important determinative factors, epimerite and spores, are unknown and so the determination cannot be absolute.

ASTEROPHORA PHILICA (Leidy) Crawley

[Figures 78, 113]

1889	*Gregarina philica*	Leidy	1889:9-10
1903	*Asterophora philica*	Crawley	1903:53
1913	*Anthorhynchus philicus*	Ellis	1913b:280

Asterophora: Sporonts solitary, very elongate. Length 300 to 2000μ. Maximum width 150μ. Ratio length protomerite : total length :: 1 : 10 to 1 : 15; width protomerite : width deutomerite :: 1 : 1.3. Protomerite conical, sharply pointed when deprived of epimerite, longer than wide. Constriction at septum not deep. Deutomerite widest at shoulder, tapering from thence to an attenuated, sharply pointed posterior extremity. Epimerite a circular, flattened cushion with a fluted periphery, situated upon a short neck at the apex of the protomerite. Endocyte and nucleus not described.

Cyst and spores not known.

Taken at Philadelphia, Pa. Host: *Nyctobates pennsylvanica* de-Geer *(N. pennsylvanicus)*. Habitat: Intestine.

The above description is taken from Leidy (1889). He remarks that

"– – the epimerite consists of a horizontal circular disc with a round milled border."

In a review of Leidy's Mss., Crawley found three more drawings from the same beetle. Crawley's words concerning his disposition of the same are as follows:

"Asterophora philica Leidy.

Gregarina philica Leidy (1889, p. 9, 1 Fig.)

It is impossible to give a description of this species. Figs. 31 and 32 are

very plainly of the same gregarine, whereas Fig. 33 seems almost certainly to belong to a different species. Further, the form figured by Leidy in 1889 is not so closely like that shown by Figs. 31 and 32 as to render it certain that the two are the same.

I therefore include the three different forms under the same name, giving only the figures and reference, until such time as sufficient material is obtained to determine accurately what the actual facts may be.

The gregarines figured were about 300 microns long."

It is evident that the form figured by Leidy (1889; my figure 113) and in his Mss. (my figure 78), are the same species. The proportions agree, the shapes of the protomerite are very similar, and the epimerite shown on figure 78 coincides with Leidy's description of the epimerite.

Crawley's figure 32 (my figure 104), may or may not be a cephalont of the same species, but the figure 33 (my figure 105), is obviously unlike and must be placed among the uncertain species. (See group at end of chapter).

Ellis placed the species in the genus Anthorhynchus, but the epimerite, as described by Leidy, coincides with Labbé's description of the genus Asterophora (1899:22):

"Épimérite en forme de bourrelet circulaire à côtes saillantes radiees en portant qu centre un mammelon saillant. Sporadin – – – allongée,"

except that Leidy does not mention the central papilla. The description of the genus Anthorhynchus does not fit the case (Labbé 1899:19):

"Epim. en gros bouton cannelé."

ASTEROPHORA CRATOPARIS Crawley

[Figure 77]

1903	*Asterophora cratoparis*	Crawley	1903:54
1913	*Anthorhynchus cratoparis*	Ellis	1913b:279

Asterophora: Length 540μ. Width not given. Ratio length protomerite : total length :: 1 : 5; width protomerite : width deutomerite :: 1 : 1.1. Protomerite nearly reniform with conical projection at apex upon which rests the epimerite. Protomerite 1.5 times as wide as high. Deep constriction at septum. Deutomerite widest at shoulder, tapering thence and terminating bluntly. Epimerite consisting of a number of "ribs projecting from a central knob." Endocyte not described. Nucleus spherical, with one karyosome.

Cysts and spores unknown.

Taken at Swarthmore, Pa. Host: *Cratoparis lunatus* Fab. Habitat: Intestine.

Ellis removed this species from the genus in which it was first placed, and included it among the members of the genus Anthorhynchus. This genus and Asterophora are differentiated by the character of the epimerite and spores. In our present discussion, the latter factor may be omitted since the spores are not known. The epimerite of Anthorhynchus is a large canaliculated button; that of the Asterophora consists of a circular cushion with a central knob and with a fluted, crenulate periphery. Crawley's species, therefore, coincides with the latter description and should be returned to that genus.

BELOIDES FIRMUS (Léger) Labbé

[Figures 116, 214]

1892	*Xiphorhynchus firmus*	Léger	1892:137-9
1899	*Beloides firmus*	Labbé	1899:26-7

Beloides: Sporonts solitary, elongate. The adults 80μ in length. Protomerite conical, dilated in center, constriction at septum. Deutomerite widest at shoulder, tapering to a sharp point. Ratio length protomerite : total length :: 1 :3.8; width protomerite : width deutomerite :: 1 : 1.2. Nucleus elongate ellipsoidal, with several karyosomes. Epimerite a stalked globose papilla with 12 large lateral curved spines and a long rigid central style (80μ long in adults).

Cysts spherical, 180 – 200μ in diameter, dehiscence by simple rupture, biconical, 14.5 by 6μ.

Taken at Poitiers, France. Host: *Dermestes lardarius* L., larva. Habitat: Intestine.

BELOIDES TENUIS (Léger) Labbé

[Figure 117]

1892	*Xiphorhynchus tenuis*	Léger	1892:139
1899	*Beloides tenuis*	Labbé	1899:26-7

Beloides: Sporonts solitary, elongate. Epimerite a stalked globular papilla, with 12 stiff lateral curved spines surmounted by a long slender sinuous style.

Cysts spherical, spores biconical, pointed.

Taken at Poitiers, France. Host: *Dermestes undulatus* Brahm, larva. Habitat: Intestine.

Labbé changed the genus name of this and the foregoing species because of priority.

BOTHRIOPSIS HISTRIO Schneider

[Figures 79, 81]

1875	*Bothriopsis histrio*	Schneider	1875:596
1892	*Bothriopsis histrio*	Léger	1892:136-7
1903	*Bothriopsis histrio*	Crawley	1903:54-5

Bothriopsis: Sporonts solitary, maximum length 425μ. Width not given. Ratio length protomerite : total length sporont :: 1 : 1.6. Width protomerite : width deutomerite :: very variable. Length of protomerite more than half that of the whole sporont. Septum strongly convex upward into protomerite. Deutomerite stout, spindle shaped, ending in a sharp point. Epimerite a small flattened disc from which project a half dozen long slender filaments. Nucleus ovoidal, generally placed diagonally, containing several karyosomes. Endocyte yellow in young, brownish black in adults.

Cysts spherical, 400 to 500μ. Spores obese, biconical, 7.2 by 5μ.

Taken at Paris and Tourraine, France, and at Wyncote, Pa. Hosts: *Hydaticus cinereus,* larv.; *Colymbetes fuscus; Acilius sulcatus;* and *Dytiscus* sp. larv. Habitat: Intestine.

Schneider stated that this species is highly polymorphic, and he described two varieties, the type form and a variety *marginata,* which is more active. He found no epimerite, but this was discovered later by Léger, who described it as consisting of six slender filaments, 80 – 90μ long. Léger also discovered the spores.

Crawley's observations on this species vary somewhat from those of Schneider; for instance, he says:

"– – – the protomerite is a large rounded mass, but whereas Schneider's figures represent it to be solid, I find that it contains, at least in some cases, a large cavity. Within this cavity was a fluid in which floated a few granules. – – – the septum dips backward. In a number of cases, however, the septum dipped forward, and such appears to be the only condition seen by Schneider. – – –."

Crawley found that in the stained specimens the protomerite is more densely granular than the deutomerite.

BOTHRIOPSIS TERPSICHORELLA (Ellis) Watson

[Figure 80]

1913	*Legeria terpsichorella*	Ellis	1913b:276
1916	*Bothriopsis terpsichorella*	Watson	(This paper)

Bothriopsis: Sporonts solitary, average length 720μ. Width 145μ. Ratio length protomerite : total length :: 1 :1 to 1.8 : 1. Ratio width pro-

tomerite : width deutomerite :: 1.3 : 1. Protomerite equal to or longer than deutomerite, the anterior fourth hemispherical to subglobose, below which is an elevated flange-like portion, remaining two thirds cylindrical. No constriction at septum. Septum projecting forward into protomerite like the finger of a glove. Deutomerite ovoidal, tapering, bluntly pointed posteriorly. Endocyte dense, homogeneous, light brown.

Cysts and spores not known.

Taken at Douglas Lake, Mich. Host: *Hydrophilus* sp. Habitat: Intestine.

This species was described by Ellis as a member of the genus Legeria. His description is as follows:

"Epimerite not seen; sporonts extremely active, constantly changing the shape of the anterior three-fifths of the body and proceeding rather rapidly in a serpentine path as a result, the protomerite often being bent almost forty-five degrees from the main axis of the body; expanded individual with a protomerite equal to or longer than the deutomerite, the anterior fourth of the protomerite hemispherical to subglobose, below which is an elevated flange-like portion, remaining two thirds cylindrical, the posterior portion with a cup-shaped depression some 60° deep into which the anterior conical portion of the deutomerite fits; deutomerite excepting the portion included by the protomerite ovoid, rather sharply rounded posteriorly; average sporonts 720μ in length; – – –."

A comparison of figure 82, a copy of *Legeria agilis* (Schn.) Labbé with figure 80, Ellis' species in question, reveals differences in the two. The genus Legeria is characterized by: a) deutomerite spindle shaped(same as in Bothriopsis) ; b) protomerite much less than half the total length; c) protomerite cylindrical, dilated in anterior third, terminating in a simple obtuse angled cone; d) septum broadly convex upward into the protomerite in the shape of an hemisphere; e) nucleus spherical; f) agility of movement not confined to protomerite, but equally active in both segments. The species in question does not belong in this genus for the protomerite occupies more than half the total length, it does not terminate in a cone, the septum is not broadly dome shaped and movement is not equally active throughout the sporont.

Bothriopsis is diagnosed by Schneider as having a) an unusually well developed protomerite consisting of a large polymorphic mass convex or concave at its anterior end and nearly or equally as long as, or longer than, the deutomerite, cylindrical in posterior two thirds; b) a septum invaginated into the protomerite like the finger of a glove; c) an ellipsoidal nucleus; d) endocyte yellow to dark brown; e) agility of movement chiefly confined to the protomerite.

The species in question coincides with the genus Bothriopsis in these characteristics: 1) polymorphism chiefly confined to anterior three

fifths of body; 2) protomerite equal to or longer than deutomerite; 3) protomerite largest in anterior third, posterior two thirds cylindrical; 4) septum invaginated into protomerite for the posterior third of its length; 5) endocyte light brown.

I have therefore changed the name of the species to *Bothriopsis terpsichorella.*

LEGERIA AGILIS (Schneider) Labbé

[Figure 82]

1875	*Dufouria agilis*	Schneider	1875:595-6
1899	*Legeria agilis*	Labbé	1899:24

Legeria: Sporonts solitary; measurements not given. Ratio length protomerite : total length :: 1 : 2.5 to 1 : 3. Width protomerite : width deutomerite :: 1.1 : 1. Protomerite irregularly cylindrical, considerably dilated in anterior third, terminated by an obtuse angled cone as wide as high. No constriction at septum. Septum convex upward into protomerite. Deutomerite irreguarly cylindrical, tapering from middle to a sharp point. Nucleus spherical, containing several karyosomes.

Cysts spherical, dehiscing by simple rupture. Spores cylindro-biconical.

Taken at Paris. Host: *Colymbetes* sp. larv. Habitat: Intestine.

PHIALOIDES ORNATA (Léger) Labbé

[Figures 87, 88]

1892	*Phialis ornata*	Léger	1892:135
1899	*Phialoides ornata*	Labbé	1899:24

Phialoides: Sporonts solitary, rather obese. Average length 1200μ. Width not given. Ratio length protomerite : total length :: 1 : 3.3; width protomerite : width deutomerite :: 1 : 1.2. Protomerite subglobular, as wide as high, constriction at septum. Deutomerite broadly ellipsoidal, widest in middle, broadly rounded behind. Epimerite persistent, a long slender cylinder, nearly as long as the whole sporont (exclusive of the epimerite), terminating in a dome shaped retractile structure surrounded by a thickened collar, above which is a ring of fine triangular chitinous teeth. Nucleus spherical, containing several karyosomes.

Cysts spherical, 300 to 400μ in diameter, dehiscing by simple rupture. Spores biconical, swollen in middle, 10.5 by 6.75μ.

Taken at Poitiers, France. Host: *Hydrophilus piceus* (L.) larv. Habitat: Intestine.

Labbé included with this species, as a synonym, Kölliker's *Gregarina brevirostra* (1848:12), probably because of the similarity in hosts. Kölliker's species shows a 'proboscis' as does Léger's, but one much shorter and differently shaped. The former is a short xiphoid cone, only half the length of the protomerite; the latter a long cylindrical process, three times the length of the protomerite. The latter is retractile, but Kölliker does not mention that this is true of his species. His drawing does not indicate the circular distal collar armed with teeth. I am inclined to think the species are quite distinct, and have therefore placed Kölliker's species in the genus Stylocephalus. For further description, see under the heading *Stylocephalus brevirostris* (Kölliker).

PILEOCEPHALUS BERGI (Frenzel) Labbé

[Figure 83]

1892	*Gregarina bergi*	Frenzel	1892:286
1899	*Pileocephalus bergi*	Labbé	1899:20

Pileocephalus: Sporonts solitary, barrel shaped. Length of largest 330μ, width 90μ. Ratio length protomerite : total length :: 1 : 5.2; width protomerite : width deutomerite :: 1 :1.6. Protomerite hemispherical, evenly rounded, 1.7 times wider than high, slight constriction at septum. Deutomerite broadly ellipsoidal, wider in middle, broadly rounded, nearly flattened posteriorly. Epimerite a large hyaline centrally dilated and sharply pointed cone half the length of the whole cephalont without the epimerite. Nucleus spherical with one large karyosome. Endocyte dense, gray to black.

Cyst and spores unknown.

Taken at Cordoba, Argentina. Host: *Necrobia ruficollis* Fabr. *(Corymetes ruf.)*. Habitat: Intestine.

PYXINIA RUBECULA Hammerschmidt

[Figures 119, 159]

1838	*Pyxinia rubecula*	Hammerschmidt	1838:357
1848	*Actinocephalus rubecula*	Frantzius	1848:193, 195
1851	*Gregarina rubecula*	Diesing	1851:12
1863	*Gregarina rubecula*	Lankester	1863:95
1892	*Pyxinia rubecula*	Léger	1892:140
1899	*Pyxinia rubecula*	Labbé	1899:26

Pyxinia: Sporonts solitary, obese. Measurements not given. Ratio protomerite : total length :: 1 : 3.6. Width protomerite : width deutomerite :: 1 : 1.2. Protomerite large, regularly conoidal, a little longer than wide (1.2 : 1), constriction at septum. Deutomerite conical, widest at shoulder, tapering to a slender, pointed extremity. Endocyte dense, of protomerite much less dense. Nucleus ellipsoidal.* Epimerite situated upon a short neck, urn-shaped, wide mouthed, crenulate on the periphery, with a short, stout conical style projecting upward through the center.

Cysts spherical, 250 to 280μ in diameter, spores bluntly biconical, 14 by 7μ.

Taken at ———?, Germany, and at Poitiers, France. Hosts: *Dermestes lardarius* L. larva and *D. vulpinus* Fabr. adult.

PYXINIA CRYSTALLIGERA Frenzel

[Figures 84, 85, 86]

1892	*Pyxinia crystalligera*	Frenzel	1892:314-29

Pyxinia: Sporonts solitary, elongate. Maximum length 750μ. Width not given. Ratio length protomerite : total length :: 1 : 5 to 1 : 10; width protomerite : width deutomerite :: 1.1 : 1. Protomerite spherical in adults. Deutomerite of adults regularly cylindrical, tapering in posterior third to a long, slender, bluntly pointed extremity. Epimerite a short sharp rigid style resting upon a small crenulate corona, the whole superimposed upon the cone shaped protomerite of the cephalont. Endocyte containing large, strongly refractile variously shaped crystals and granules of pyxinin. Nucleus irregularly ellipsoidal, containing several karyosomes.

Cyst and spores not known. Taken at Cordoba, Argentina. Hosts: *Dermestes vulpinus* Fabr.; *Dermestes peruvianus* Casteln., adults and larvae of both. Habitat: Intestine.

*Frantzius' illustration shows a spherical nucleus.

PYXINIA FRENZELI Laveran and Mesnil

[Figure 89]

1900 *Pyxinia Frenzeli* Laveran and Mesnil 1900:554-7

Pyxinia: Sporonts solitary, obese. Length 200μ. Maximum length of cephalonts 150μ. Maximum width 40μ. Cephalonts only illustrated. Ratio length protomerite : total length :: 1 : 4; width protomerite : width deutomerite :: 1 : 2. Protomerite (of cephalonts) cylindrical to subglobose, constricted at septum. Deutomerite subglobose, nearly as wide as long. Epimerite in two parts, a slender cylindrical base equal in length to protomerite, and superimposed upon same, and a short, sharp, apical style equal in length to the cylinder. Nucleus spherical, containing a large karyosome.

Cysts not seen; spores ovoidal, 14 by 6μ.

Taken at Paris. Hosts: *Attagenus pellio* (*Dermestes* sp.). Habitat: Intestine.

PYXINIA MÖBUSZI Léger and Duboscq

[Figures 97, 98]

1900 *Pyxinia Möbuszi* Léger and Duboscq 1900:1566
1902 *Pyxinia Möbuszi* Léger and Duboscq 1902:409-18

Pyxinia: Sporonts solitary. Length 100 to 140μ. Width not given. Ratio length protomerite : total length :: 1 : 5 to 1 : 6. Width protomerite : width deutomerite :: 1 : 1. Protomerite hemispherical, lower margin straight, projecting beyond deutomerite at septum. Deutomerite regularly cylindrical, ending in a blunt point or in a well rounded extremity. Epimerite persistent, a long slender sinuous style attached to base of the epithelial cell, i. e., to mesothelial wall, of the host, extending through this cell, longitudinally, to lumen, the cephalont body remaining in lumen, beyond cilia. Epimerite as long or longer than the whole cephalont itself. Endocyte containing paramylin granules and small yellow refractile bodies. Nucleus spherical, with one karyosome and several chromatic granules.

Cysts spherical, 60 to 70μ in diameter. Spores elongate, barrel shaped, 6.5 by 7μ long.

Taken at Grenoble (?), France. Host: *Anthrenus verbasci* Olivier, larv. (*A. verbasci* L.) Habitat: Intestine.

STICTOSPORA PROVINCIALIS Léger

[Figures 90, 91]

1893	*Stictospora provincialis*	Léger	1893:129-31
1896	*Stictospora provincialis*	Léger	1896:32
1899	*Stictospora provincialis*	Labbé	1899:21

Stictospora: Sporonts, solitary, elongate: Length 1000 to 2000μ. Width not given. Ratio length protomerite : total length :: 1 : 6. Width protomerite : width deutomerite :: 1 : 1.2. Protomerite subglobular, terminating in a broadly conical anterior extremity. Width equal to height. Deep constriction at septum. Deutomerite widest at shoulder, tapering to a slender, sharply pointed distal portion. Nucleus ellipsoidal, with several karyosomes, epimerite consists of a short stalked, globular papilla depressed anteriorly, there proceeding from the depression a dozen long, backwardly directed, sharply pointed processes which fit closely around the papilla and completely cover it. Protoplasm of anterior end of protomerite yellow.

Cysts spherical, 800μ in diameter, dehiscence by simple rupture; spores biconical, slightly curved.

Taken near Marseilles, France. Hosts: Larvae of *Melolontha* sp. and *Rhizotrogus* sp. Habitat: Intestine.

But one species is known in this genus and in the sub-family Stictosporidae.

STEININA OVALIS (Stein) Léger and Duboscq

[Figures 92, 93, 94]

1838	*Clepsidrina polymorpha*	Hammerschmidt	1838:355
1848	*Stylorhynchus ovalis*	Stein	1848:182-223
1848	*Stylorhynchus ovalis*	Frantzius	1848:195
1851	*Gregarina ovalis*	Diesing	1851:9
1863	*Gregarina polymorpha*	Lankester	1863:95
1875	*Clepsidrina polymorpha*	Schneider	1875:580-2
1902	*Gregarina polymorpha*	Berndt	1902:405
1904	*Steinina ovalis*	Léger and Duboscq	1904:352-5
1910	*Steinina ovalis*	Pfeiffer	1910:108

Steinina: Sporonts solitary, obese. Length 100μ. Width not given. Ratio length protomerite : total length :: 1 : 2.5; width protomerite : width deutomerite :: 1 : 1.4. Protomerite cylindrical, terminat-

ing in a large cone, as broad as high, no constriction at septum. Deutomerite short, ovoidal, nearly as wide as long, terminating in an obtuse angled cone. Nucleus spherical and containing one large karyosome. Epimerite a short retractile digitiform process which later becomes a flattened button. Cysts spherical or ovoidal, 100μ in diameter, dehiscing by simple rupture. Spores biconical, broad through middle, 9 by 7.5μ.

Taken in France. Host: *Tenebrio molitor* L. larva. Habitat: Intestine.

This is a much discussed and confused species. Early writers grouped together all the polycystid gregarines found in the larva of *Tenebrio molitor* as one species. Hammerschmidt evidently actually found several species for he named the one species he described *Clepsidrina polymorpha*. Stein differentiated three species and separated out this one, even assigning to it a different genus than the other two, *C. polymorpha* and *C. cuneata*.

Schneider described under the name *Clepsidrina polymorpha* (Hamm.) three species, one of them being the *Stylorhynchus ovalis* of Stein. His words are as follows:

"L'espèce *Clepsidrina polymorpha* â été instituèe par Hammerschmidt, et plus tard démembrée par Stein, qui trouva moyen d'établir à ses dépens trois espèces dont une fut reportee dans le genre Stylorhynchus.

Ce preténdu *S. ovalis* est simplement le céphalin de l'une des variétes que nous allons décrire."

Berndt, in a long paper on the Gregarines of *Tenebrio molitor* larva, still considered this species the cephalont of *G. polymorpha* in 1902.

It remained for Léger and Duboscq (1904) to clear up the discussion. They created a new genus for this species, and called it Steinina.

STEININA OBCONICA Ishii

[Figure 95]

1914 *Steinina obconica* Ishii 1914:439-41

Steinina: Sporonts solitary, obese. Length 120 to 140μ. Width 68 – 80μ. Ratio length protomerite : total length :: 1 : 5 to 1 : 7. Width protomerite : width deutomerite :: 1 : 1. Protomerite dome-shaped, three times as wide as high. Septum constricted slightly at periphery. Deutomerite widest just below septum, and tapering to a slender, bluntly pointed posterior extremity. Epimerite a short conical hyaline projec-

tion 1/4 as long as the protomerite is high. Endocyte dense. Nucleus spherical.

Cysts spherical to slightly ovoidal, 120 by 108μ. Spores unknown.

Taken in the Province of Izu, Japan. Host: *Tribolium ferrugineum* F. Habitat: Intestine.

The character of the epimerite is evidence that this species is rightly placed.

STEININA ROTUNDA Watson

[Figure 173]

1915 *Steinina rotunda* Watson 1915:32-3

Host: *Amara angustata* Say. Taken at St. Joseph, Ill., November, 1914. Habitat: Intestine.

A dozen individuals were found in a single host. The sporonts are solitary, the body stout, short and broad. The epimerite persists even on some of the largest individuals. It is a spherical, sessile or shortly stalked and hyaline knob. The protomerite just below it is broadly conical in shape, widening rapidly downward to form a cylinder bulging in the middle portion. A deep constriction is present at the septum. The protomerite is widest three fourths of its length from the anterior end, and, without the epimerite, it is as high as wide. The deutomerite is practically spherical except in its anterior end, which, at the septum, is more or less flattened or sometimes concave downward. The deutomerite widens rapidly from the septum and is as wide as long.

In color, the body is light brown or tan, of equal density in both protomerite and deutomerite; the protoplasm is homogeneous and not very abundant. The anterior half of the protomerite and the epimerite is transparent. The nucleus is visible in vivo in specimens of all ages. In all the specimens attached to the epithelium, no matter how large, the nucleus contains but one karyosome; in the free individuals, no matter how small, a large number of small deeply staining chromosomes are present. The epicyte is thin and of equal width throughout. Longitudinal striations are visible.

Most of the specimens seen possessed epimerites, whether free or attached. A goodly number of these, however, were free in the lumen. The epimerite disappears by being gradually constricted off. When the specimens are on a slide in a water medium for fifteen minutes, approximately, the epimerite breaks, the supposition being that it is highly porous and the sudden strain caused by media of unequal density outside and inside is reduced by the bursting of this fragile structure. When

the trophozoite is attached, only the epimerite is embedded and the free ends of several cells are destroyed by the parasite.

Very slow movement of progression was noted. The power of contraction seems to be centered in the anterior part of the deutomerite, for the parasite is able to contract this portion of the body into a narrow neck.

This species is very probably a member of the genus Steinina, family Actinocephalidae, although the cysts and spores are not known. The globular hyaline epimerite corresponds to that of one stage of the epimerite of the type species, *Steinina ovalis,* as described by Léger and Duboscq (1904:352-4). The incipient stylous epimerite and the hat shaped end stage were not observed in this species. The adults are non-associative and in shape of the deutomerite, of the protomerite, and the conoidal anterior projection of the protomerite, together with the nuclear shape and content, coincide with those of the type species. Coupling of sporonts takes place probably just previous to cyst formation and not, as in the genus Gregarina, near the beginning of sporont life.

Some of the important measurements are given below; all dimensions are expressed in microns:

Total length sporont	250	220	180
Length protomerite with epimerite	130	105	70
Length epimerite	20	20	15
Length protomerite without epimerite	110	85	56
Length deutomerite	120	115	110
Width protomerite	130	90	70
Width deutomerite	150	120	85
Ratio			
length protom. (without epimerite) : total length	1 :2.3	1 :2.5	1 :3.3
width protom.: width deutomerite	1 :1.1	1 :1.3	1 :1.2
Diameter nucleus	40	32	40

STEININA HARPALI NOV. SPEC.

[Figures 256-59, 269]

Host: *Harpalus pennsylvanicus longior* (Kirby).

Location, Urbana, Ill., June, 1915.

The parasites were found in the coelom, attached to the intestinal walls of several beetles. The sporonts are solitary, small and obese. The maximum recorded length is 200μ, the average length 150μ, and the maximum width 100μ. The ratio of length protomerite : total length without primite :: 1 : 3 to 1 : 5 and the average ratio of width protomerite :

width deutomerite :: 1 : 1.3. The protomerite is cone-shaped, constricted above the middle, and terminates in almost every instance in a small epimerite. This structure in youngest individuals is a simple short spike; as the animal grows older it becomes a sphere, and finally becomes cup shaped. Old sporonts sometimes lose this epimerite. The protomerite is widest at the septum and there is here a slight constriction which may, however, be lacking. The deutomerite is ovoidal, widest at the shoulder just below the septum, and terminates in a broadly rounded or slightly tapering posterior end. The nucleus is visible in young individuals as a minute spherical body.

The protoplasm is dense in the deutomerite, being black in transmitted light; it is nearly as dense in the lower half of the protomerite, but the upper portion of the latter is nearly devoid of endoplasm. The epimerite is clear.

Cysts are dense, spherical and average 120μ in outer diameter. The inner diameter is approximately 90μ. Spores were not seen.

Figures for a few individuals measured are as follows; dimensions are given in microns:

Total length sporont	200	150	105
Length protomerite with epimerite	80	65	50
Diameter epimerite	20	20	18
Length protomerite alone	60	45	32
Length deutomerite	120	85	70
Width protomerite	90	50	105
Width deutomerite	100	80	105
Ratio			
length protom. (without epimerite) : total length	1 :3.3	1 :3.3	1 :3.3
width protom. : width deutomerite	1 :1.1	1 :1.6	1 :1

This species differs from the other species found in the genus Harpalus as follows: *Gregarina parva* (Crawley) Watson and *Hirmocystis harpali* Watson are both associative; *Actinocephalus gimbeli* (Ellis) Watson differs in size and proportions (the epimerite was not seen in the latter species); in *Actinocephalus harpali* (Crawley) the maximum length of the sporonts is 1200μ, and in proportions and sizes of cysts (640μ in the latter), the two species are widely different.

The species is placed in the genus Steinina because the epimerite is a short mobile digitiform process changing through a sphere into a flattened button; the sporonts are small, solitary and obese; the protomerite terminates in a large cone; the cysts are small.

It differs sufficiently in size range from the three other species described in this genus to be designated a separate species.

STYLOCYSTIS ENSIFERA (Ellis)

[Figures 96, 99]

1912	*Stylocephalus ensiferus*	Ellis	1912a:686-7
1913	*Stylocystis ensiferus*	Ellis	1913b:274

Stylocystis: Sporonts solitary, short. Average length 40 to 65μ. Ratio length protomerite : total length :: 1 : 3; width protomerite : width deutomerite :: 1 : 1 to 1 : 4. Protomerite cylindrical, conical to subglobose. Approximately as wide as high. Deep constriction at septum in adults. Deutomerite half as wide as long, widest at shoulder, tapering slightly and ending in a flattened or very broadly rounded posterior extremity. Epimerite a stout style, equal to protomerite in length. Endocyte dark gray, opaque. Nucleus not seen.

Cyst and spores not known.

Taken at Quirigua, Guatemala. Host: *Leptochirus edax* Sharp. Habitat: Intestine.

Ellis first described this species as a member of the family Stylocephalus, later removing it to the family Actinocephalidae.

CYSTOCEPHALUS ALGERIANUS Schneider

[Figures 115, 160]

1886	*Cystocephalus algerianus*	Schneider	1886:100
1899	*Cystocephalus algerianus*	Labbé	1899:31

Cystocephalus: Sporonts solitary, ovoidal. Length 3 to 4 mm. Ratio length protomerite : total length :: 1 : 6; width protomerite : width deutomerite :: 1 : 1.7. Protomerite dome shaped, widest at base, twice as wide as high, no constriction at septum. Deutomerite ovoidal, widest through middle, length less than width, posterior end conical, sharply pointed. Epimerite placed upon a short collar, globose, with conical apex. Nucleus elongate ellipsoidal, containing several karyosomes.

Cysts not known. Spores irregularly and peculiarly shaped, 10 by 10.5μ.

Taken in Algeria. Host: *Pimelia* sp. Habitat: Intestine.

LOPHOCEPHALUS INSIGNIS (Schneider) Labbé

[Figures 110, 114, 161]

1882	*Lophorhynchus insignis*	Schneider	1882:435
1885	*Lophorhynchus insignis*	Schneider	1885:14
1899	*Lophocephalus insignis*	Labbé	1899:31

Lophocephalus: Sporonts solitary, very elongate. Length 1000μ. Width not given. Ratio length protomerite : total length :: 1 : 15; width protomerite : width deutomerite :: 1 : 1.3. Protomerite subglobose, flattened, twice as wide as high, constriction at septum. Deutomerite cylindrical, widest at end of anterior third, flattened at posterior extremity. Nucleus of sporont spherical with one karyosome. Epimerite a large flattened disc, depressed slightly in center, crenulate on periphery, longitudinally striated and carrying at base a circle of very many short upwardly directed digitiform processes. The cephalont which possesses the circular disc-shaped epimerite spherical or nearly so. Its nucleus with a coiled chromatin band.

Cysts subspherical or subovoidal, 430 by 330μ in diameter, dehiscing by pseudocyst. Spores extruded in chains, irregularly hat-shaped, 10μ long.

Taken at Tours, Indre-et-Loire, France. Host: *Helops striatus*. Habitat: Intestine.

OOCEPHALUS HISPANUS Schneider

1886	*Oocephalus hispanus*	Schneider	1886:101
1899	*Oocephalus hispanus*	Labbé	1899:32

Epimerite a sphere carried on a short conical neck. Host: *Morica* sp. Habitat: Intestine.

Ellis (1913b:282) includes this genus with Cystocephalus under the name of the latter. The two genera are, however, distinct, having epimerites different in shape; the former being globular, set on a short conical neck, the latter spade-shaped (in side view), i. e. dilated in middle portion and conical at apical end, set on a short cylindrical slender collar.

STYLOCEPHALUS OBLONGATUS (Hammerschmidt) Watson

[Figures 106, 120]

1838	*Rhiziniaoblongata*	Hammerschmidt	1838:357
1848	*Sporadina oblongata*	Frantzius	1848:195
1851	*Gregarina oblongata*	Diesing	1851:14
1875	*Stylorhynchus oblongatus*	Schneider	1875:569
1882	*Stylorhynchus oblongatus*	Schneider	1882:434
1916	*Stylocephalus oblongatus*	Watson	(This paper)

Stylocephalus: Sporonts solitary, elongate. Maximum length 3000μ; width not given. Ratio length protomerite : total length :: 1 : 6 to 1 : 8. Ratio width protomerite : width deutomerite :: 1 : 2. Protomerite globular, constriction at septum. Deutomerite cylindrical, tapering slightly from middle, ending in a rather slender blunt posterior extremity. Epimerite a thick cylindrical neck with a terminal dilated portion with papilla on extremity. Whole epimerite equal to 1.5 to twice the length of protomerite alone. Endocyte yellow in cephalont, becoming black in adult sporont. Nucleus ellipsoidal, with several karyosomes.

Cysts irregularly spherical with slight depressions and protuberances. Spores brown, united in chains, 7μ in long axis.

Taken at Paris and Poitiers, France. Hosts: *Opatrum sabulosum* (L.) and *Asida grisea* (F.) Habitat: Intestine.

Because the name was preoccupied, Ellis renamed the genus Stylorhynchus, Stylocephalus. The species thus becomes *Stylocephalus oblongatus.*

STYLOCEPHALUS LONGICOLLIS (Stein) Watson

[Figures 107, 121]

1815	*Gregarina* sp.	Gaede	1815:17
1848	*Stylorhynchus longicollis*	Stein	1848:222
1848	*Stylorhynchus longicollis*	Frantzius	1848:195
1851	*Gregarina Mortisagae*	Diesing	1851:12
1863	*Gregarina longicollis*	Lankester	1863:95
1875	*Stylorhynchus longicollis*	Schneider	1875:572
1882	*Stylorhynchus longicollis*	Schneider	1882:423
1884	*Stylorhynchus longicollis*	Schneider	1884:1-36
1916	*Stylocephalus longicollis*	Watson	(This paper)

Stylocephalus: Sporonts solitary, elongate. Measurements not given. Ratio length protomerite : total length :: 1 : 10; width protome-

rite : width deutomerite :: 1 : 1.1. Protomerite pentagonal in lateral optical view, truncate at apex, slight constriction at septum, width equal to length. Deutomerite elongate, cylindrical, tapering in posterior two thirds and ending in a rather blunt point. Nucleus ellipsoidal, with several karyosomes. Endocyte dense. Epimerite consisting of a long slender cylindrical neck, terminating in a slightly dilated papillate anterior end, the whole three or four times the length of the protomerite alone.

Cysts irregularly spherical, surface covered with small indentations and papillae. Spores like those of *S. oblongatus.*

Taken at Paris. Host: *Blaps mortisaga.* Habitat: Intestine.

STYLOCEPHALUS BREVIROSTRIS (Kölliker) Watson

[Figure 118]

1848	*Gregarina brevirostra*	Kölliker	1848 :12
1848	*Stylorhynchus brevirostris*	Frantzius	1848 :195
1851	*Gregarina brevirostrata*	Diesing	1851 :9
1863	*Gregarina brevirostris*	Lankester	1863 :95
1899	*Phialoides ornata*	Labbé	1899 :24
1916	*Stylocephalus brevirostris*	Watson	(This paper)

Stylocephalus: Sporonts solitary, stout bodied. Ratio length protomerite : total length :: 1 : 4; width protomerite : width deutomerite :: 1 : 1.2. Protomerite cylindrical, of nearly equal width throughout, width equal to length, no constriction at septum, corners rounded at anterior end. Epimerite a small xiphoid conoidal tongue projecting upward from center of protomerite, length equal to half that of protomerite. Deutomerite just below septum a little wider than protomerite, tapering to a rather sharp point. Nucleus spherical, with six to nine small karyosomes. Cyst and spores unknown.

Taken at ———, Germany. Host: *Hydrophilus* sp. larva. Habitat: Intestine.

Kölliker illustrated another figure of this species besides the one copied in figure 118, in which the whole body is less angular in outline (1848, Pl. 2, Fig. 15) ; the epimerite is a sphere, the protomerite nearly so also, and the deutomerite ellipsoidal with a well rounded posterior extremity. The animal is drawn under abnormal conditions, however, a drop of egg albumen having been used as a medium and the animal left in it for some time.

Frantzius placed this species where it evidently belongs, in the genus Stylocephalus, then called Stylorhynchus. His definition of the genus is "Einzeln lebend mit russelartigem Kopfanhang."

Labbé regarded the species identical with *Phialoides ornata,* probably because of an identity of hosts rather than a similarity of parasites. A table of the important characteristics of the two species follows, and speaks for itself.

	St. brevirostris	*Ph. ornata*
Epimerite	1/2 length of protomerite	3 x length of protomerite
length	1/8 length of whole sporont	Equal to whole sporont without epimerite
width	1/4 that of protomerite	1/10 that of protomerite
shape	Xipho-conical, i. e. elongate-conoidal, dilated in middle	Cylindrical
apex	Pointed	Flattened, a thickened collar, thickly set with 20 (more or less) small teeth
Protomerite		
shape	Widest at shoulder, tapering to posterior end	Ellipsoidal
where widest	Anterior 1/5	Central region
Posterior extremity	Tapering and pointed	Broadly rounded
Nucleus		
shape	Spherical, several karyosomes	Spherical, several karyosomes.

As noted above, Ellis (1912:25) changed the name of the genus from Stylorhynchus to Stylocephalus, hence this name changes also.

STYLOCEPHALUS GLADIATOR (Blanchard) Watson

1905	*Stylorhynchus gladiator*	Blanchard	1905:923-8
1916	*Stylocephalus gladiator*	Watson	(This paper)

Stylocephalus: Sporonts solitary, elongate, average length 300 to 400μ, maximum length 720μ, width 30μ, maximum width 70μ. Protomerite short, globular. Deutomerite elongate cylindrical, with a slender attenuated posterior extremity, bluntly pointed. Epimerite in two parts, a very long slender cylindrical neck and a dilated xiphoid-shaped apical portion, often longer than the whole gregarine. Nucleus ovoidal with one large karyosome. Cysts not seen.

Taken at Grenoble, France. Host: *Helenophorus collaris* L. Habitat: Intestine.

STYLOCEPHALUS GIGANTEUS Ellis

[Figures 108, 109]

1912	*Stylocephalus giganteus*	Ellis	1912:25-27

Stylocephalus: Sporonts solitary, elongate. Length 1200 to 1800μ. Width not given. Ratio length protomerite : total length :: 1 : 9 to 1 : 18; width protomerite : width deutomerite :: 1 : 1 to 1 : 1.5. Protomerite dome shaped, widest at base or dome shaped, dilated above base, flattened anteriorly. Constriction at septum. Deutomerite widest at shoulder. Cylindrical, terminating in an abrupt but sharply pointed cone. Epimerite a long pointed cone, situated upon a conoidal projection of the protomerite of the cephalont. Endocyte dense. Nucleus not described.

Cysts spherical, 450μ in diameter, entire surface papillated and indented, dehiscence by pseudocyst, spores extruded in chains. Spores irregularly subspherical, black, 7 by 11μ.

Taken at Boulder, and at Denver, Colo. Hosts: *Eleodes* sp.; *Asida opaca* Say; *Asida* sp. and *Eusattus* sp. Habitat: Intestine.

SPHAERORHYNCHUS OPHIOIDES (Schneider) Labbé

1886	*Sphaerocephalus ophioides*	Schneider	1886:100
1899	*Sphaerorhynchus ophioides*	Labbé	1899:32

Sphaerorhynchus: Sporonts solitary, elongate. Length 3 to 4 mm. Epimerite 1/6 the total length of cephalont, consisting of a small spherical or ovoidal body carried on a long cylindrical stalk, broadest at base and gradually narrowing toward apical end. Cephalonts 1.3 mm. long, 220μ of which is length of epimerite and 8.5μ for the terminal sphere.

Taken at ————————. Host: *Acis* sp. Habitat: Intestine.

ACANTHOSPORA PILEATA Léger

[Figures 162, 215]

1892	*Acanthospora pileata*	Léger	1892:145-6
1899	*Acanthospora pileata*	Labbé	1899:28

Acanthospora: Sporonts solitary, elongate. Length 300 to 400μ. Ratio length protomerite : total length :: 1 : 6; width protomerite : width deutomerite :: 1 : 1.5. Protomerite nearly hemispherical, little higher than wide, constricted at septum. Deutomerite elongate ellipsoi-

dal, widest just anterior to middle. Endocyte brown. Epimerite a broadly conical papilla. Nucleus ellipsoidal, with several karyosomes.

Cysts spherical, 150 – 180μ in diameter. Spores biconical, ends truncate, with six equatorial spines in a circle. Dimensions 7.5 by 10.5μ.

Taken in the Department of Poitou, France. Hosts: *Cistelides* sp.; *Omoplus* sp. larva (Scudder gives a genus Omophlus, not Omoplus). Habitat: Intestine.

ACANTHOSPORA POLYMORPHA Léger

[Figure 163]

1896	*Acanthospora polymorpha*	Léger	1896:44-46
1899	*Acanthospora polymorpha*	Labbé	1899:28

Acanthospora: Sporonts solitary, elongate, polymorphic. Maximum length 1000μ. Protomerite irregularly cylindro-conical. Deutomerite ovoidal, widest through middle. Endocyte yellowish brown.

Cysts 500 to 700μ in diameter. Spores bipyramidal, each face hexagonal, each pole armed with 6 short spines and with a circle of 6 equatorial spines, 8 by 4.4μ.

Taken in Poitou and Tourraine, France. Host: *Hydrous caraboides* (L.) larva. Habitat: Intestine.

ANCYROPHORA GRACILIS Léger

[Figures 122, 164]

18—	*Gregarina acus*	Stein	18—:—
1848	*Actinocephalus Acus*	Frantzius	1848:195
1863	*Gregarina acus*	Lankester	1863:95
1892	*Ancyrophora gracilis*	Léger	1892:146-7

Ancyrophora: Sporonts solitary, elongate. Maximum length 2000μ; maximum width 400μ. Protomerite conical, dilated in central region. Constriction at septum. Deutomerite widest at shoulder, tapering to a long acuminate posterior extremity. Nucleus spherical, with several karyosomes. Epimerite a globular papilla with 8 long backwardly directed flexible 'tentacles'.

Cysts spherical, 200μ in diameter. Spores biconical, truncate, with four spines at each pole and six equatorial spines, 8.5 by 5.1μ.

Taken at ———, Germany, and Poitiers, France. Hosts: *Carabus* sp.; *Carabus auratus* L.; *C. violaceus* L., larvae and adults; and *Silpha thoracica* L. larva.

This species was first described by Stein under the name *Gregarina acus,* according to Léger, but no mention is made of the species in Stein's 1848 article. Frantzius and Lankester refer the species to Stein; Diesing does not mention it.

If the originally described species is the same as the species described by Léger in 1892 under the name *Ancyrophora gracilis,* then the name of the latter should be changed to *A. acus* (Stein) Léger. In the absence, however, of complete data, it stands as given by Léger.

ANCYROPHORA UNCINATA Léger

[Figure 216]

1892	*Ancyrophora uncinata*	Léger	1892:147-8

Ancyrophora: Sporonts solitary, length 150 to 200μ. Width not given. Epimerite garnished with 12 rigid hooks in two alternate rows.

Cysts spherical. Spores spined, both polar and equatorial, 7.5 by 4.5μ.

Taken at Poitiers, France. Hosts: *Dytiscus* sp.; *Colymbetes* sp.; *Sericostoma* sp.; and *Limnophilus rhombicus* (L.) *(Phryganea rhomb.).* Habitat: Intestine.

Labbé placed *Gregarina Dytiscorum* Frantz. with this species under the name of the latter, evidently from a similarity in the first host given above. The species are, however, unlike and I have separated them, listing the former among Uncertain Species, under the Actinocephalidae.

The last three hosts given by Léger are not Coleoptera but Neuroptera and the circumstance of finding the same species of gregarine in such widely separated hosts is unusual and almost unique, yet the record is authentic.

COMETOIDES CAPITATUS (Léger) Labbé

[Figures 123, 124, 165]

1892	*Pogonites capitatus*	Léger	1892:150-1
1899	*Cometoides capitatus*	Labbé	1899:29

Cometoides: Sporonts solitary, elongate. Length 1500μ. Width not given. Ratio length protomerite : total length :: 1 : 13; width protomerite : width deutomerite :: 1 : 1.5. Protomerite subspherical, width equal to height. Constriction at septum. Deutomerite widest at shoulder, tapering from thence to a very long slender bluntly pointed posterior extremity. Epimerite globose, stalked, armed with a sub-

equatorial band of 12 to 15 long slender flexible filaments 32 to 35μ long. Nucleus spherical, with several karyosomes.

Cysts spherical, 300μ in diameter, dehiscence by simple rupture, spores cylindro-biconical, apices truncate, each face octagonal. Poles armed with four spines each, two equatorial rows of spines, spores 2.5 by 5.1μ.

Taken at Poitou and Avanton, France. Host: *Hydrous* sp. larva. Habitat: Intestine.

COMETOIDES CRINITUS (Léger) Labbé

[Figure 125]

1892	*Pogonites crinitus*	Léger	1892:149-50
1899	*Cometoides crinitus*	Labbé	1899:29

Cometoides: Sporonts solitary, very elongate. Maximum length 2000μ. Ratio length protomerite : total length :: 1 : 20; ratio width protomerite : width deutomerite :: 1 : 1.3. Body shaped very similarly to *C. capitatus* except that it is longer. Epimerite hemispherical, flattened surface upward, armed with an equatorial ring of 6 or 8 long slender flexible filaments 100μ long. Endoplasm brown. Nucleus ellipsoidal, with several karyosomes.

Cysts spherical, 200 to 300μ in diameter. Spores cylindro-biconical, spines at the poles and in two equatorial bands.

Taken at Poitou and Vendee, France. Host: *Hydrobius* sp. larva. Habitat: Intestine.

CORYCELLA ARMATA Léger

[Figures 111, 112, 166]

1892	*Corycella armata*	Léger	1892:144-5

Corycella: Sporonts solitary, 280 to 300μ long. Ratio length protomerite : total length :: 1 : 4; width protomerite : width deutomerite :: 1 : 0.9. Protomerite subglobular, constriction at septum, wider in middle than deutomerite. Deutomerite widest at shoulder, tapering thence to a sharp point. Endoplasm gray brown. Epimerite a large globular papilla set upon a stout cylindrical collar which is two-thirds as long as the protomerite itself, and armed with 8 strong short sharply pointed recurved and backwardly directed hooks. Nucleus spherical, containing several karyosomes.

Cysts spherical, 250μ in diameter. Spores biconical, truncate, 4 small spines at each pole, no equatorial spines. 13 by 6.5μ.

Taken at Poitou, France. Host: *Gyrinus natator* (L.) larva. Habitat: Intestine.

HYALOSPORA ROSCOVIANA Schneider

[Figure 129]

1875 *Hyalospora roscoviana* Schneider 1875:584

Hyalospora: Sporonts biassociative, cylindrical, very elongate. Length and width not given. Ratio length protomerite : total length primite :: 1 : 9; width protomerite : width deutomerite :: 1 : 1.6. Protomerite of primite cylindrical, conical, rounded at anterior extremity, twice as high as wide, a constriction at septum. Deutomerite elongate cylindrical, tapering but slightly at posterior end and terminating in a rounded extremity. Nucleus elongate ellipsoidal, with one large karyosome. Epimerite not known. Endocyte yellow to yellow-orange.

Cysts spherical (?), dehiscing by simple rupture. Spores broadly ellipsoidal but sharply pointed.

Taken at Roscoff, France. Host: *Petrobius maritimus.*

The name Petrobius has been applied to genera of both Orthoptera (Thysanura) (1817) and Coleoptera (1836) and, not knowing which one Schneider found as host, I have included this species among the Coleopteran as well as among the Orthopteran parasites. Schneider says of the habitat:

> "Les Petrobius se recontrent, en effet, sur le mur même qui separe le laboratoire de la mer, tapis dans les interstices des pierres. La même espèce est commune sur une grande partie du littoral – – –".

From its habitat, the host might be either an Orthopteran or a Coleopteran.

This is the only species in the genus Hyalospora.

SPHAEROCYSTIS SIMPLEX Léger

[Figure 137]

1892 *Sphaerocystis simplex* Léger 1892:115-16

Sphaerocystis: Sporonts solitary, subspherical, length 100 to 140μ. Width not given. Dicystid, having protomerite only when young. Shape

spherical, with a large papillate extension at each end. Nucleus spherical, with a large karyosome.

Cysts spherical, 100μ in diameter, without spore ducts. Encystment solitary. Spores ovoidal, 10.5 by 7.5μ.

Taken at Iteuil (Poitou), France. Host: *Cyphon pallidulus* Boh. *(C. pallidus)*. Habitat: Intestine.

EUSPORA FALLAX Schneider

[Figure 131]

1875	*Euspora fallax*	Schneider	1875:583

Euspora: Sporonts biassociative, ellipsoidal. Measurements not given. Ratio length protomerite : total length primite :: 1 : 6; width protomerite : width deutomerite :: 1 : 2.5. Protomerite of primite spherical, deep constriction at septum; deutomerite ellipsoidal, widest through middle or just posterior to middle, posterior end flattened. Nucleus spherical with one karyosome. Endocyte dense except in anterior third of protomerite, where there is a distinct conoidal area of less dense endocyte.

Cysts spherical, dehiscing by simple rupture. Spores prismatic, square cornered, pentagonal in optical view.

Taken at Roscoff, France. Host: A Melolonthid (*Rhizotrogus aes-Asida servillei* Soll. Habitat: Intestine.

HIRMOCYSTIS ASIDAE Léger

1896	*Eirmocystis asidae*	Léger	1896:30
1899	*Hirmocystis asidae*	Labbé	1899:13

Hirmocystis: Sporonts very small, bi- or tri-associative. Cylindrical. Maximum length of association of two, 20μ. Width not given. Ratio length protomerite : total length primite :: 1 : 10 to 1 : 12; width protomerite : width deutomerite :: 1 : 2. Protomerite subglobular, depressed. Deutomerite elongate cylindrical. Epimerite a small simple hyaline papilla. Myocyte well developed. Nucleus spherical with one small karyosome.

Cysts spherical, 70μ, dehiscence by simple rupture. Spores cylindro-ovoidal, 6 by 3.5μ.

Taken at Ain-Fezza, Tlemcen, Province of Oran, Algeria. Host: *Asida servillei* Soll. Habitat: Intestine.

HIRMOCYSTIS HARPALI NOV. SPEC.

[Figures 265, 266, 267, 268, 273, 274]

Host: *Harpalus pennsylvanicus erythropus* (Dej.).

Location Urbana, Illinois, June, 1915.

This species was found very abundant in the intestines of four beetles examined, one containing at least a thousand associations. The sporonts were found in linear associations of twos, threes and fours and each sporont is elongate cylindrical in shape. The maximum length of associations found was 1060μ, maximum length of sporonts 560μ, and maximum width 80μ. Ratio length protomerite : total length :: 1 : 7; ratio width protomerite : width deutomerite :: 1 : 1.2. The protomerite of the primite is dome shaped, a little wider than long and constricted at the septum, but not deeply so. The deutomerite is elongate, seven times as long as the protomerite and well rounded at the posterior end. The protomerite of the satellite is very much flattened, twice as wide as high and not deeply constricted at the septum. The primite fits into a very deep concavity in the protomerite of the satellite (See Fig. 274).

The protoplasm is very dense, black in the deutomerite and much less dense, and tan in color, in the protomerite. The nucleus is spherical and contains one karyosome visible in adults as a clear spot.

The epimerite is large and spherical (Fig. 268). Myonemes are very conspicuous as a horizontal network. Cysts were not seen.

A few measurements are as follows, all dimensions being given in microns:

Total length of associations	1060	910	730
Primite:			
Length protomerite	80	60	60
Length deutomerite	480	440	300
Width protomerite	70	60	50
Width deutomerite	80	90	60
Total length sporont	560	500	360
Ratio			
length protom.: total length	1:7	1:8.3	1:6
width protom.: width deutomerite	1:1.1	1:1.5	1:2
Nucleus, diameter		50	

Satellite:				
Length protomerite	50	40	30	
Length deutomerite	450	370	340	
Width protomerite	90	50	60	
Width deutomerite	80	70	90	
Total length sporont	500	410	370	
Ratio				
length protom.: total length	1:10	1:10	1:12	
width protom.: width deutomerite	1:9	1:1.4	1:1.5	
Length associations of more than two sporonts				
Primite	300	140	120	110
First satellite	170	150	140	100
Second satellite	190	140	70	70
Third satellite		130		
Total length of association	660	560	330	280

This species is very peculiar in that two distinct types of specimens are encountered, viz. large sporonts 500μ long associated in twos (association 1000μ in length), and very small sporonts 100μ long associated in threes and fours. A chain of three of the smaller sporonts seldom exceeds half the length of a chain of two of the larger type. One chain of four small individuals measured only 560μ long.

That the two types of sporonts, however, represent a single species is shown by the following facts: (a) one or two of the smaller sporonts are often attached as satellites to a sporont of the larger type; (b) intermediate sizes are found between the small and the large sporonts; and (c) the small and large sporonts are identical in shape and proportions. Since associations are generally composed entirely of one type of individuals, the difference is not a sexual one.

This species is very similar in shape and proportions and the deep concavity of the protomerite of the satellite to *Gregarina serpentula* de Magalhaes, from *Gryllus domesticus*. The sporonts of the latter occur, however, in twos, while the former occur in threes and fours and it therefore belongs to a different genus entirely.

The species differs considerably from any previously described from the host genus Harpalus. It is differentiated from *Gregarina parva* (Crawley) Watson, *Actinocephalus gimbeli* (Ellis) Watson and *A. harpali* (Crawley) in both measurements and proportions and in the fact that the latter two species are solitary while this one is associative.

GREGARINA CUNEATA Stein

[Figures 132, 133, 134, 135, 136, 152]

1838	*Clepsidrina polymorpha*	Hammerschmidt	1838:357
1848	*Gregarina cuneata*	Stein	1848:209-10,222
1848	*Gregarina cuneata*	Frantzius	1848:196
1851	*Gregarina cuneata*	Diesing	1851:13
1863	*Gregarina polymorpha*	Lankester	1863:95
1875	*Clepsidrina polymorpha* var. *cuneata*	Schneider	1875:581
1899	*Gregarina polymorpha* var. *cuneata*	Labbé	1899:11
1902	*Gregarina cuneata*	Berndt	1902:393-404
1903	*Gregarina xylopini*	Crawley	1903:47
1904	*Gregarina cuneata*	Léger & Duboscq	1904:354-5
1910	*Clepsidrina cuneata*	Pfeiffer	1910:108
1911	*Gregarina cuneata*	Ishii	1914:435
1914	*Gregarina cuneata*	Ishii	1914:435

Gregarina: Sporonts biassociative, elongate cylindrical. Length 380μ; width 170μ. Ratio length protomerite : total length primite :: 1 : 3; width protomerite : width deutomerite primite :: 1 : 1.5. Protomerite elongate cylindrical, 2½ times as wide as posterior portion, dilated at anterior end, widest part acutely angled, apex broadly rounded. Slight constriction at septum. Deutomerite elongate, width gradually increases from septum to posterior portion, terminates in a very broadly rounded extremity. Nucleus spherical, small, with one karyosome.

Cysts spherical, 240μ in diameter, long spore ducts. Spores extruded in chains, doliform, 5.7 by 4μ.

Taken at Roscoff and Caen, France; Berlin; Philadelphia; and in the province of Izu, Japan. Host: *Tenebrio molitor* L. larv. and adult. Habitat: Intestine.

Hammerschmidt described two gregarines from *Tenebrio molitor* under one name, *Clepsidrina polymorpha*. He regarded them as different shapes assumed by the same parasite.

Stein said, concerning his discoveries:

> "Ich fand drei verschiedend Formen, von denen zwei zur Gattung Gregarina in engern Sinne, eine zur Gattung Stylorhynchus gehort. Hammerschmidt kannte wahrscheinlich bereits zwei Formen, doch geht dies selbst aus seinen Abbildungen die gar zu roh sind, nicht mit volliger Bestimmtheit hervor; er hielt sie aber für eine Art und nannte sie *Clepsidrina polymorpha*."

Stein's figure is reproduced in Figure 133.

Frantzius enumerated among his species both *G. polymorpha* and *G. cuneata* Stein, not recognizing that the former included the latter. He did not illustrate the species *Gregarina cuneata,* but included under the name *G. polymorpha* one excellent figure of *G. cuneata* (Fig. 135). Stein said that Frantzius knew all three gregarines in this Tenebrio, but

"– – wirt sie ebenfalls zu einer Art unter dem Namen *Gregarina polymorpha* zusammen blos aus dem Grunde, weil sie in einem und demselben Thiere leben."

He named one of the species *Stylorhynchus ovalis.* The other two

"– – sind einander sehr ahnlich und fast gleich gross. Die eine ist durch den nach vorn erweiterten, flach gedruckten, keilähnlichen Kopf, der fast ⅓ der Lange des Leibes gleichkommt, und durch den nach hinten erweiterten Leib ausgezeichnet; ich nenne sie *Gregarina cuneata.*"

Lankester placed this species and Schneider's *St. ovalis* together as synonyms under the name *Gregarina polymorpha* Hamm. Schneider grouped together under the name *Clepsidrina polymorpha* (Hamm.) the three species from *Tenebrio molitor,* which Stein had separated some twenty-five years before. He designated the species which is under discussion as *Clepsidrina polymorpha* var. *cuneata* (Stein). He considered adult associations of *G. cuneata* as young immature associations of *G. polymorpha.*

"Les jeunes individus sont nombreux et remarquables par le volume relatif de leur protomerite (Fig. 16 et 17)."

The figure 16 referred to is a typical association of *G. cuneata.* He says further

"– – Resemble beaucoup à la précédente; est arrondie en arriere au deutomérite et plus massive dans son ensemble (Fig. 11, le primite.)".

His figure 11, my figure 132, coincides with Stein's figure of his *G. cuneata,* my figure 133. Berndt studied the gregarines of the larva of *Tenebrio molitor* and isolated *G. cuneata* from the others. Léger and Duboscq (1904) confirmed his work. (Their drawing is reproduced in my figure 152).

In Leidy's unpublished manuscript, Crawley (1903) found two drawings of gregarines taken from the Tenebrionid, *Xylopinus saperdioides.* One has been otherwise disposed of, but one drawing is of a species identical with or very similar to *G. cuneata.* No description or measurements accompanied the drawings. From a similarity of the figures of the type *G. cuneata* and the figure given by Crawley (my figure 134), the species is the same.

Ishii (1911:279 and 1914:435) found the species in Japan (my figure 36) in *Tribolium ferrugineum,* one of the Tenebrionidae, and very

similar to *Tenebrio molitor*. It is quite possible that the parasite is not identical with or a variety of the classic *G. cuneata*, for the figure does not exactly coincide with the others, but no data whatever accompanies the figures and it seems best to leave the species in the present position.

GREGARINA POLYMORPHA (Hammerschmidt) Stein

[Figures 140, 141, 142, 153]

1838	*Clepsidrina polymorpha*	Hammerschmidt	1838:357 ?
1848	*Gregarina polymorpha*	Stein	1848:210,222
1848	*Gregarina polymorpha*	Frantzius	1848:193,195
1851	*Gregarina polymorpha*	Diesing	1851:13
1875	*Clepsidrina polymorpha*	Schneider	1875:580
1899	*Gregarina polymorpha*	Labbé	1899:10
1902	*Gregarina polymorpha*	Berndt	1902:404-8
1904	*Gregarina polymorpha*	Léger and Duboscq	1904:354-7
1910	*Clepsidrina polymorpha*	Pfeiffer	1910:108
1911	*Gregarina polymorpha*	Ishii	1911:279

Gregarina: Sporonts biassociative, elongate, cylindrical, maximum length 350μ, maximum width 100μ. Ratio length protomerite : total length :: 1 : 5 to 1 : 7; width protomerite : width deutomerite :: 1 : 1.8 to 1 : 2. Protomerite dome shaped, as wide as high, no constriction at septum. Deutomerite elongate cylindrical, rounded at posterior extremity. Nucleus small, spherical, one karyosome.

Cyst and spores unknown.

Taken at Berlin, Germany, and Roscoff and Grenoble, France. Host: *Tenebrio molitor* L. larva and adult. Habitat: Intestine.

Hammerschmidt knew two of the forms of gregarines parasitic in the larvae of *Tenebrio molitor*. He called them, however, by one name. In the words of Stein,

> "Hammerschmidt kannte wahrscheinlich bereits zwei dieser Formen, – –; er hielt sie aber für eine Art und nannte sie *Clepsidrina polymorpha*."

Stein differentiated the two species, calling one *G. cuneata*, my figure 133, the other *G. polymorpha*, my figure 142.

Frantzius gave, side by side, figures of Stein's *G. cuneata* and *G. polymorpha*, and called them both *G. polymorpha*. (Pl. VII, group V, Figs. 1 and 2; my figures 135 and 140).

Lankester mentioned *G. polymorpha* and under this name gave as synonyms *Stylorhynchus ovalis* Stein and *G. cuneata* Stein.

Schneider brought together again in coincidence with Hammer-

schmidt's original determination, the three species which Stein had differentiated, and added another variety. He described 1) *Clepsidrina polymorpha* var. *cuneata,* 2) *C. polymorpha typica,* 3) *C. mimosa,* and 4) disposes of *Stylorhynchus ovalis* Stein as

"– – simplement le céphalin de l'une des varietes que nous allons décrire."

Of these forms, the first has been designated *Gregarina cuneata* Stein; the second remains *Gregarina polymorpha;* the third has been dropped as an authentic species for it is obviously immature and probably from its shape a young individual of *G. cuneata;* the fourth is now *Steinina ovalis* (Stein) Léger and Duboscq.

Berndt separated the species *G. polymorpha* from *G. cuneata,* describing each in detail. Léger and Duboscq corroborated his work and created the genus Steinina for the species previously known as *Stylorhynchus ovalis* Stein. Ishii found the species in Japan, from one of the Tenebrionidae. No description of adults is given.

GREGARINA AMARAE Frantzius

1838	*Clepsidrina ovata*	Hammerschmidt	1838:356
1848	*Gregarina amarae*	Frantzius	1848:195
1851	*Gregarina Amarae*	Diesing	1851:12
1863	*Gregarina Amarae*	Lankester	1863:94
1899	*Gregarina amarae*	Labbé	1899:36

This parasite has not been found since the original discovery of Hammerschmidt. Frantzius mentioned it by name only; Diesing gave this description:

"Gregarina Amarae Frantzius.

Proboscis – – – Receptaculum ovatum breve. Corpus subglobosum. Longit. 9/40''', crassit – – –

Clepsidrina ovata Hamm. (Individua bina postice juncta)". – – –. Habitaculum *Amara cuprea,* in intestinus tenuibus (Hamm.)."

Labbé says that the host is probably the beetle known now as *Poecilus cupreus* (L.).

That this species is a member of the genus Gregarina is attested by Diesing's words "Individua bina postice juncta" which indicates the biassociative nature of the sporonts. No drawing accompanies any available mention of the species.

GREGARINA TENUIS Hammerschmidt

1848	*Gregarina tenuis*	Frantzius	1848:195
1851	*Gregarina tenuis*	Diesing	1851:13
1863	*Gregarina tenuis*	Lankester	1863:94

Host: *Allecula* sp.

No mention is made of this species among those in Labbé's Sporozoa or in the list of Sporozoa in Lankester's Treatise (1903). The species is probably a true Gregarina, for Frantzius included in this genus only gregarines "– – stets zu zweien aneinandergeheftet."

He credits the discovery of the species to Hammerschmidt.

GREGARINA ELONGATA Frantzius

[Figure 154]

1848	*Gregarina elongata*	Frantzius	1848:193,195
1851	*Gregarina elongata*	Diesing	1851:13
1863	*Gregarina elongata*	Lankester	1863:94

Host: *Crypticus* sp.

This species is well illustrated by Frantzius. It does not appear in Labbé's Sporozoa.

GREGARINA SCARABAEI Lankester

1851	*Gregarina Scarabaei relicti*	Leidy	1851:208,287
1863	*Gregarina Scarabaei*	Lankester	1863:94

This species is known only from the original description, which is as follows:

"Body cylindro-fusiform. Superior division presenting four sides of a hexahedron, subacute. Nuclear body of inferior division transparent, globular or elliptical, containing several coarse granules. Length from 1/66 to ¼ lines; head 1/400 in. to 1/133 in. long, by 1/285 in. to 1/111 in. broad. Anterior portion of inferior division 1/200 in. to 1/86 in. broad, posterior division 1/666 in. to 1/250 in. broad. Longitudinal lines of inferior division more distinct than those of upper division, 1/8000 in. apart."

No drawing accompanies the description.

Host: *Scarabaeus relictus* larva.

This species takes the first binomial name applied to it, that of Lankester.

GREGARINA PASSALI Lankester

[Figure 139]

1853	*Gregarina passali cornuti*	Leidy	1853:238
1863	*Gregarina Passali*	Lankester	1863:94
1903	*Gregarina passali cornuti*	Crawley	1903:45
1913	*Gregarina passali cornuti*	Ellis	1913a:201

Gregarina: Sporonts biassociative, cylindrical. Length of associations 350 to 400μ. Width not given. Ratio length protomerite : total length primite :: 1 : 5; width protomerite : width deutomerite :: 1 : 1. Protomerite dome shaped, flattened, 1½ times as wide as high. Slight constriction at septum. Deutomerite cylindrical, sometimes constricted a little in middle. Posterior extremity broadly rounded or flattened. Endocyte opaque; nucleus spherical, content not mentioned.

Taken at Philadelphia, Pa., and New Orleans, La. Host: *Passalus cornutus* Fab. Habitat: Intestine.

Leidy's figure represents sporonts with the deutomerite much wider than long. Crawley's figure is normal. Leidy probably left the animals on the slide in a water medium until they had become greatly distended before drawing them. Ellis recovered the same species from the same Lucanid, from Louisiana.

This species takes the first binomial name, that of Lankester.

The beetles of this host species at Urbana, Illinois, seem to be uninfected. Twenty-five or more have been examined without finding an instance of parasitism with gregarines. They are abundantly supplied with nematodes.

GREGARINA MELOLONTHAE Lankester

1856	*Gregarina Melolonthae Brunneae*	Leidy	1856:47
1863	*Gregarina Melolonthae*	Lankester	1863:94
1913	*Gregarina melolonthaebrunneae*	Ellis	1913b:269

Gregarina: Sporonts biassociative, ellipsoidal. Length of primite 400μ, width 250μ. Ratio length protomerite : total length :: 1 : 4; width protomerite : width deutomerite :: 1 : 1.7. Protomerite oblate spheroidal, slightly elevated at summit. Deutomerite oblong ovoidal. Taken at Philadelphia, Pa.

Host: *Melolontha brunnea.* Habitat: Intestine.

This species has not been redescribed. No drawings accompany Leidy's brief record. Lankester shortened the name to a binomial and it is this name by which the species must be designated. Ellis merely mentions the species.

GREGARINA MUNIERI (Schneider) Labbé

[Figures 128, 147]

1875	*Clepsidrina Munieri*	Schneider	1875:574-8
1899	*Gregarina munieri*	Labbé	1899:9-10

Gregarina: Sporonts biassociative, elongate ellipsoidal. Length and width not given. Ratio length protomerite : total length primite :: 1 : 6 to 1 : 7; width protomerite : width deutomerite :: 1 : 7. Protomerite cylindrical, flattened anteriorly, a little wider than high, less than 1.5 times, slight constriction at septum. Deutomerite cylindrical, ending bluntly or tapering slightly from middle and ending in a broad but rather pointed extremity. Epimerite a small spherical papilla situated upon the apex of a short conical projection of the protomerite of the cephalont. Endocyte reddish orange. Nucleus spherical, with one karyosome.

Cysts ovoidal. Spore ducts 3 to 6, reddish, very short, less than the radius of the cyst in length. Spores extruded in chains, spores barrel shaped, cylindrical, dilated through middle, terminating bluntly.

Taken at Roscoff, France. Hosts: *Timarcha tenebricosa* (F.); *Chrysomela violacea* (Goeze) and *C. haemoptera* L. Habitat: Intestine.

Schneider's argument concerning the species in question speaks for itself and is quoted here (1875:575):

"'Dans le tube alimentaire de divers Coleoptères, notamment du *Lucanus parallelopipedus,* de plusieurs Mélasomes et de la *Timarcha tenebricosa,* j'ai trouvé abondamment une espèce de Vers intestinaux, dont je joins ici le dessin.' Dufour, 1826. 'L'espèce que j'ai dit habiter des entrailles de divers Coléoptères, mérite, à cause de sa forme, le nom Conica.' Dufour, 1828. Si maintennant on se reporte à la figure indiquée par L. Dufour, on n'y trouve pas la designation de l'hôte de l'individu répresenté; la légende portant simplement cette mention: 'Vers intestinaux trouves dans le tube alimentaire de divers Coleopteres.' Il n'y a donc aucun indice que l'auteur ait plus particulierement visé l'espèce qui nous occupe, et comme il cite d'abord le *Lucanus parallelopipedus,* c'est à la Grégarine de ce Mélolonthide qu'il conviendra de réserver l'épithète de Conica. Quant à l'espèce actuelle, je l'ai dédiée à mon excellent ami M. Munier Chalmas – – –."

The species which Dufour found in *Lucanus parallelopipedus* is the species now named *Actinocephalus conicus* (Dufour) Frantzius.

GREGARINA LAUCOURNETENSIS (Schneider) Labbé

1885	*Clepsidrina Laucournetensis*	Schneider	1885a:28
1899	*Gregarina laucournetensis*	Labbé	1899:11

Gregarina: Sporonts biassociative, obese. Length 60 to 70μ; width 50 – 60μ. Cysts spherical, one spore duct. Spores elongate ovoidal, extruded in chains.

Taken at ————————? Host: *Parnus* sp. Habitat: Intestine.

GREGARINA STATIRAE Frenzel

[Figure 138]

1892	*Gregarina statirae*	Frenzel	1892:234-82

Sporonts biassociative, spheroidal. Length 300 to 350μ. Width 200μ. Ratio length protomerite : total length primite :: 1 : 5; width protomerite : width deutomerite :: 1 : 3.5. protomerite hemispherical, widest at base, 1.7 times as wide as high. Deutomerite spherical, as wide as high. Nucleus spherical, with one karyosome. Endocyte dense except in anterior third of protomerite, where it is sparse. Epimerite a simple short cylindrical papilla rounded at apex.

Spores and cysts unknown.

Taken at Cordoba, Argentina. Host: *Statira unicolor* Blanch. Habitat: Intestine.

GREGARINA LONGIROSTRIS (Léger) Labbé

[Figure 155]

1892	*Clepsidrina longirostris*	Léger	1892:122-4
1899	*Gregarina longirostris*	Labbé	1899:12

Gregarina: Sporonts biassociative, obese. 100μ long. Ratio length protomerite : total length :: 1 : 4; width protomerite : width deutomerite :: 1 : 1.1. Protomerite conoidal, dilated in posterior half. No constriction at septum. Protomerite obovoidal. Nucleus spherical with one karyosome. Epimerite an elongate simple cylinder, 50 – 60μ long, one half or more than half as long as whole cephalont. Endoplasm greenish yellow.

Cysts ovoidal, 60 to 70μ in diameter. One spore duct. Spores barrel shaped, 7.4 by 3.8μ.

Taken in the valley of the Loire, France. Host: *Thanasimus formicarius* (L.). Habitat: Intestine.

GREGARINA ACUTA (Léger) Labbé

[Figure 217]

1892	*Clepsidrina acuta*	Léger	1892:121-2
1899	*Gregarina acuta*	Labbé	1899:11

Gregarina: Sporonts biassociative. Protomerite short, cylindrical, rounded in front. Deutomerite cylindrical, rounded behind. Nucleus spherical, with one karyosome. Epimerite a sharp point.

Cyst and spores unknown.

Taken at Poitou, France. Host: *Trox perlatus* Scriba. Habitat: Intestine.

GREGARINA STEINI Berndt

[Figure 146]

1902	*Gregarina steini*	Berndt	1902:408-13

Gregarina: Sporonts biassociative, 42 to 150μ in length, width 16 to 30μ. Protomerite hemispherical. Constriction at septum. Deutomerite widest at shoulder, tapering to a more or less slender but well rounded posterior extremity. Epimerite a simple globular papilla.

Cysts ovoidal, 70 to 100μ by 85 to 160μ. Cysts smaller than those of *G. cuneata* or *G. polymorpha*.

Taken in Berlin, Germany. Host: *Tenebrio molitor* L. larva. Habitat: Intestine.

The work on this species needs confirmation before it can be accepted absolutely. Léger and Duboscq (1904:351-60) described the gregarines of the larva of this beetle but made no mention of this species. No one of the previous workers on the same beetle has mentioned it. Not knowing how polymorphic *G. polymorpha* may be, the present writer does not wish to comment on this species.

GREGARINA PARVA (Crawley) Watson

[Figure 130]

1903	*Gigaductus parvus*	Crawley	1903a:633-4
1913	*Gigaductus parvus*	Ellis	1913b:271
1916	*Gregarina parva*	Watson	(This paper)

Gregarina: Sporonts biassociative, length 150μ; width 90μ. Ratio length protomerite : total length :: 1 : 5; width protomerite : width

deutomerite :: 1 : 1.1 Protomerite subglobular, somewhat flattened anteriorly. Widest through middle portion. Width 1½ times height. Deep constriction at septum. Deutomerite elongate ellipsoidal, widest about or little above middle, terminating bluntly. Nucleus large, spherical, content not noted. Endocyte coarsely granular, not dense.

Cysts 170 to 200μ in diameter, spherical, dehiscence by "one enormous spore duct." Spores cylindrical, 25 by 10μ, square cornered.

Taken at Wyncote, Pa., and Vincennes, Ind. Hosts: *Harpalus caliginosus* Fab. and *H. pennsylvanicus* Dej. Habitat: Intestine.

Crawley created a genus Gigaductus for this species. The genus is described thus:

"Cysts spherical, with a thin gelatinous envelope. Dehiscence by one enormous spore duct. Maturation period short. Spores cylindrical, very large. Wall single, thick. Spores marked with diagonal lines, those on one side opposed in direction to those on the other, giving the spore a latticed appearance. These lines are apparently due to the sporozoites, which make up a hollow cylinder lying in contact with the inner surface of the spore wall. The residuum, an ellipsoidal mass liberally provided with granules, occupies the cavity of this hollow cylinder."

I have placed the species in question under the genus Gregarina. Several hitherto described species of the genus Gregarina have been recorded to dehisce by one spore duct (e. g. *G. laucournetensis; G. longirostris).* It is to be noted that sometimes cysts of the genus Gregarina develop only one spore duct and others in the same fecal mass several. There is apparently no maximum-minimum limit to the number of ducts which may be present within the same species.

GREGARINA LUCANI (Crawley) Watson

[Figure 150]

1903	*Euspora lucani*	Crawley	1903:50-1
1916	*Gregarina lucani*	Watson	(This paper)

Gregarina: Sporonts biassociative, elongate ellipsoidal. Length of associations 880μ. Primite 520μ long, 128μ wide. Ratio length protomerite : total length primite :: 1 : 10; width protomerite : width deutomerite :: 1 : 1.7. Protomerite flattened, widest through middle, twice as wide as high, deep constriction at septum. Deutomerite flattened or broadly rounded behind.

Cyst and spores unknown.

Taken at Swarthmore, Pa. Host: *Lucanus dama* Thunb. Habitat: Intestine.

Ellis (1913a:264) says:

"This species is referred to the genus Euspora because of the shape of the sporont and the coleopteran host, making the generic determination very uncertain."

The original description gives no evidence that the species is a member of the genus Euspora. The protomerite is not spherical and does not contain the conoidal, less dense area in its anterior third, and the spores are not known and cannot be verified with those of the genus Euspora. The fact that the host is a beetle is of significance since the Eusporae and the Gregarinae are both found in beetles.

I have placed the species in the genus Gregarina because it is associative and does not have characteristics of the other associative genera.

GREGARINA CAVALIERINA Blanchard

1905	*Gregarina cavalierina*	Blanchard	1905:926-8

Gregarina: Sporonts biassociative, the couple attaining a total length of 1500 to 2000μ. Length primite 500 to 1000μ, width 80 to 100μ. Ratio length protomerite : total length primite :: 1 : 15; width protomerite : width deutomerite? Protomerite flattened, ellipsoidal, longitudinal axis perpendicular to that of deutomerite. Deutomerite cylindrical, rounded hemispherically at posterior end. Endocyte yellow in protomerite, darker in deutomerite. Nucleus spherical, 27μ in diameter, one karyosome.

Cysts spherical, 400μ in diameter, dehiscing by spore ducts 200μ long, 40μ wide at base and 15μ wide at end. Spores extruded in chains. Spores ellipsoidal, 8 by 6μ.

Taken in the mountains of Maure, France. Host: *Dendarus (Pandarus) tristis* Rossi (=*coarcticollis* Mls.). Habitat: Intestine.

GREGARINA SOCIALIS Léger

1906	*Gregarina socialis*	Léger	1906:323-7
1911	*Gregarina socialis*	Sokolow	1911:279

Sokolow gives the reference to the original paper by Léger as Arch. Prot. 7:106-30, but this reference is incorrect. The brief description and text figure are buried in a paper on another species and are not indexed.

Sporonts in chain of 8 to 10 individuals; average size 100μ. Often 3 or 4 small sporonts at posterior extremity. Length protomerite : length deutomerite :: 1 : 5 or 1 : 6.

Host: *Eryx ater* Fabr. larva.

Ellis (1913c:79) refers to this paper as it is given above, but, it is obvious, did not see the paper in question.

GREGARINA GUATEMALENSIS Ellis

[Figure 144]

1912 *Gregarina guatemalensis* Ellis 1912a:687-8

Gregarina: Sporonts biassociative, the couple attaining 400 to 500μ in length. Width not given. Ratio length protomerite : total length primite :: 1 : 3 to 1 : 3.5; width protomerite : width deutomerite :: 1 : 2.5 to 1 : 7.5. Protomerite subglobose, slightly flattened and pointed at apex, faint constriction at septum. Deutomerite irregularly cylindrical, narrowest at septum, widening very gradually and greatly dilate in posterior fourth, terminating in a very broad flattened extremity, the base nearly twice as wide as the deutomerite at the septum. The whole sporont is shaped like a salt cellar. Sarcocyte very thick, especially in posterior portion of deutomerite. Endocyte of protomerite denser than that of deutomerite. Nucleus spherical, small.

Taken at Quirigua, Guatemala. Host: *Ninus interstitialis* Esch. Habitat: Intestine.

In Ellis' paper (1913b) the host genus is given as Nelus instead of Ninus as in the original description.

GREGARINA GRISEA Ellis

[Figure 151]

1913 *Gregarina grisea* Ellis 1913a:200-1

Gregarina: Sporonts biassociative, cylindrical. Length of association 500 to 1050μ. Length primite 200 to 500μ. Ratio length protomerite : total length primite :: 1 : 4.5 to 1 : 6.5. Ratio width protomerite : width deutomerite :: 1 : 1 to 1 : 5. Protomerite hemispherical, widest at posterior margin, no constriction at septum. Deutomerite cylindrical; tapering slightly to a broadly rounded posterior extremity. Endocyte dense, dark gray. Nucleus spherical.

Cyst and spores not known.

Taken at New Orleans, La. Host: *Tenebrio castaneus* Knoch. Habitat: Intestine.

GREGARINA MINUTA Ishii

[Figure 143]

1914 *Gregarina minuta* Ishii 1914:436-7

Gregarina: Sporonts biassociative, length of associations 118μ, length primite 58μ. Ratio length protomerite :: total length :: 1 : 9; width protomerite : width deutomerite :: 1 : 1.7. Protomerite somewhat flattened, rounded anteriorly, twice as wide as high. No constriction at septum. Deutomerite cylindrical, broadly rounded at posterior end. Endocyte not dense. Nucleus large, spherical, with one karyosome.

Cysts spherical, 36 by 48μ.

Taken in the province of Izu, Japan. Host: *Tribolium ferrugineum* F. Habitat: Intestine.

Under the name *Gregarina minuta,* the author described two gregarines belonging to widely different families, one, the larger, being a Didymophyes *(D. minuta),* from the absence of a protomerite in the satellite, and the other the gregarine described above. For a detailed statement of these facts, see article in appendix of this chapter.

GREGARINA KATHERINA Watson

[Figure 171]

1915 *Gregarina katherina* Watson 1915:31

Host: *Coccinella novemnotata* Herbst.

Location: Oyster Bay, L. I., August, 1914.

Percent of Infection: Fourteen lady beetles of various species were examined and only two found to be parasitized, one with this species, the other with *G. barbarara* Watson. The infection with this gregarine was very heavy, the whole alimentary tract being filled with parasites which numbered into hundreds. The gregarines were practically transparent and it was impossible to count them.

The sporonts are biassociative when adult. The shape is that of a typical gregarine of this genus. The protomerite of the primite is widest at the mass, rounded at its free ends and more or less flattened at the apex. It is 1 1/4 to 1 1/2 times as wide as high, and constricted slightly at the septum. The protomerite of the satellite is flattened top and bottom and three to four times as wide as high. Its upper and lower surfaces are about equal in width. The deutomerite is cylindri-

cal to ellipsoidal from 1-1/2 to two times as wide as is the protomerite; it terminates in a broadly rounded posterior extremity.

Color is practically absent from the animals for the body is almost transparent and contains very little protoplasm in either protomerite or deutomerite. The sporonts were stained with iodine or an anilin dye (safranin in water) before they could be studied.

The nucleus is small and spherical, in diameter attaining only 1/3 to 1/4 the width of the deutomerite. It contains one large karyosome.

Young individuals were seen attached to epithelial cells of the intestine by large smooth sessile transparent epimerites. No cysts were seen.

Movement consists of very slow progression and a still slower contortion of the body.

The character of the epimerite and the biassociative sporonts leaves no doubt that this species belongs to the genus Gregarina. It is differentiated from the other species found in the Coccinellidae by the shape and proportions of the sporonts, especially of the protomerite of the satellite, and by size.

A table of dimensions of a few associations is given here; all dimensions are expressed in microns:

Total length association	96	108	134	141	148
Primite:					
Length protomerite	9	11	10	10	11
Length deutomerite	35	59	52	59	59
Width protomerite	11	17	19	20	14
Width deutomerite	21	30	30	34	30
Total length sporont	44	70	62	69	70
Ratio					
length protom.: total length	1:5	1:1.3	1:6.2	1:6.9	1:6.3
width protom.: width deutom.	1:1.9	1:1.8	1:1.6	1:1.7	1:2.1
Satellite:					
Length protomerite	8	7	8	8	6
Length deutomerite	44	71	64	64	72
Width protomerite	14	26	20	20	21
Width deutomerite	22	35	27	30	23
Total length sporont	53	78	72	72	78
Ratio					
length protom.: total length	1:6.5	1:11	1:9	1:9	1:13
width protom.: width deutom.	1:1.6	1:1.4	1:1.3	1:1.5	1:1.1
Diameter nucleus			9	8	

GREGARINA BARBARARA Watson

[Figure 169]

1915 *Gregarina barbarara* Watson 1915:31

Host: *Coccinella* sp.

Fourteen lady beetles were examined and only two were parasitized, one with this species and the other with the preceding species. Sixteen associations of the present species were found in the one host. The region of infection is the intestine.

The adult sporonts are biassociative. In shape they are similar to other members of this genus. The primite is not essentially different in shape from that of *G. katherina*. The protomerites of the primite in the two species are identical, viz. 1 1/4 to 1 1/2 times as broad as high, cylindrical at the base and terminating in a broadly rounded, often apically flattened anterior extremity. The deutomerite of the primite of this species is more nearly globular, broadening appreciably backwards from the septum and attaining its greatest width in the middle or at the beginning of the posterior two thirds of the body. From here the deutomerite rapidly contracts, ending in a very broadly rounded and not flattened posterior end. The shape of the satellite is quite different from that of the primite. It has the form of an elongated egg smaller at the posterior end. The satellite is generally longer than but is never as wide as the primite. The protomerite is very different from that of *G. katherina*. It is approximately five times as wide as high, and twice as wide as the protomerite of the primite. It is broadly rounded in front and but imperfectly interlocked with the primite. The septum is straight or slightly concave upward, with no constriction whatever at its periphery, the protomerite and deutomerite forming a perfectly smooth contour at the edges of the septum. The deutomerite of the satellite is widest a little behind the septum and anterior to the center of the egg shaped mass. The body gradually tapers from the region of greatest width, ending in a blunt, well rounded extremity.

This parasite is practically transparent with a few large scattered darkly colored protoplasmic granules accumulated in the central regions of the deutomerite of the primite; the satellite is generally free from these dark colored inclusions. The nucleus is rarely obscured by protoplasm; it is small and spherical.

The epicyte is very thin and fragile and the animals quickly break up when exposed to the diluted digestive juices of the host.

A list of the essential measurements with dimensions in microns is appended:

Total length association	283	275	220	192
Primite:				
Length protomerite	17	22	25	20
Length deutomerite	103	113	120	105
Width protomerite	28	40	40	40
Width deutomerite	80	90	90	75
Total length sporont	120	135	145	125
Ratio				
length protom.: total length	1:7	1:6	1:5.8	1:6.2
width protom.: width deutomerite	1:2.5	1:2.2	1:2.2	1:1.9
Satellite:				
Length protomerite	17	10	18	15
Length deutomerite	46	130	57	52
Width protomerite	65	55	60	40
Width deutomerite	80	80	80	68
Ratio				
length protom.: total length	1:9.2	1:14	1:4.2	1:4.5
width protom.: width deutomerite	1:1.2	1:1.4	1:1.3	1:1.7
Diameter nucleus	10			

This species is considerably larger than *Gregarina katherina.*

GREGARINA FRAGILIS Watson

[Figure 175]

1915 *Gregarina fragilis* Watson 1915:32

Host: *Coccinella* sp.

Location: Urbana, Illinois, November, 1914.

The intestine of the host is the seat of infection. Out of thirty or more lady beetles of many species which were examined, only two yielded parasites. About twenty-five associations were found in the two hosts.

The sporonts are biassociative. The protomerite of the primite is cylindrical, rounded at the corners and nearly flattened anteriorly; it is about 1 2/3 times as wide as high. A shallow constriction or none at all is present at the septum. In the satellite, the protomerite is altered slightly in shape, being both flattened and broadened. The deutomerite is subglobular, widest in the middle or slightly posterior to the middle and terminates in a broadly rounded extremity. The satellite is smaller than the primite and less nearly globular in shape.

This parasite is often practically transparent and can only be seen after staining with iodine or a dye in water. The largest specimens contain endocyte tinged with tan color in the deutomerite, while the protomerite is invariably colorless. The nucleus is spherical and small, one third to one fourth the width of the deutomerite in its diameter; it is invisible in vivo and contains one large transparent karyosome.

Trophozoites were seen but the epimerite was not visible because of the transparency when embedded. Cysts are unknown.

Measurements of two associations are as follows; all dimensions are cited in microns:

Total length association	185	208
Primite:		
Length protomerite	20	21
Length deutomerite	80	90
Width protomerite	33	31
Width deutomerite	61	60
Total length sporont	100	111
Ratio		
length protom.: total length	1:5	1:5
width protom.: width deutomerite	1:2	1:2
Satellite:		
Length protomerite	20	20
Length deutomerite	65	77
Width protomerite	33	31
Width deutomerite	43	48
Total length sporont	85	97
Ratio		
length protom.: total length	1:4.2	1:4.8
width protom.: width deutomerite	1:1.3	1:1.5
Diameter nucleus	10	11

This species differs from the other two species described from Coccinellidae in size, shape of the protomerite of the satellite and in color.

GREGARINA TENEBRIONELLA Watson

[Figure 174]

1915 *Gregarina tenebrionella* Watson 1915:32

Host: Larva of an unidentified member of the family Tenebrionidae. Location: Urbana, Illinois, October, 1914.

The intestine of the host was heavily infected, with a hundred or more associations.

The sporonts are biassociative and the shape is that characteristic of this genius. The animals are very small and subglobular. The protomerite of the primite is as wide at the base as throughout the posterior third of the body. Its anterior end is well rounded, without a papilla at the apex. In the satellite, the width of the protomerite is about equal to the height, although it is more or less flattened top and bottom. The length of the protomerite of the primite is one fourth the total length. The deutomerite of the primite is short, broad, globose, widest through the median portion and broadly rounded behind. In the satellite it tapers slightly and is less globular in shape, being one third to four fifths as wide as the deutomerite of the primite. The primite is larger in every instance recorded than the satellite, often longer by one third.

The color of this species is pale gray. The protoplasm is not dense in any part of the body and the protomerite is almost devoid of protoplasm. The granules of the body are not homogeneous, smaller being interspersed with larger. The satellite is more nearly transparent than the primite. The nucleus is spherical, one fourth to one third the width of the deutomerite in its diameter; it is not visible in vivo in the primite but generally so in the satellite. The interlocking device between the sporonts is weakly developed and the individuals often barely touching are easily displaced. Trophozoites and cysts were not seen. Movement consists of a slow uniform progression; contortion was not noted.

A table of measurements follows, in which dimensions are given in microns:

Total length association	140	137	129	109
Primite:				
Length protomerite	17	18	15	16
Length deutomerite	53	53	46	46
Width protomerite	23	20	25	20
Width deutomerite	42	37	38	35
Total length sporont	70	70	61	62
Ratio				
length protom.: total length	1:4.1	1:3.9	1:4	1:3.9
width protom.: width deutomerite	1:1.8	1:1.8	1:1.5	1:1.7

Satellite:				
Length protomerite	13	17	18	10
Length deutomerite	57	50	50	37
Width protomerite	28	20	28	16
Width deutomerite	32	30	50	18
Total length sporont	70	67	68	47
Ratio				
length protom.: total length	1:5.4	1:4	1:3.8	1:4.7
width protom.: width deutomerite	1:1.2	1:1.5	1:1.8	1:1.1
Diameter nucleus	10	8	9	

Shape and size differentiate this species from all the other species found in the Tenebrionidae. For list of these gregarines, see Index of this chapter on Coleopteran parasites.

GREGARINA GRACILIS Watson

[Figure 170]

1915 *Gregarina gracilis* Watson 1915:32

Host: Larva of an unidentified member of the family Elateridae.

Location: Urbana, Illinois, October, 1914.

The parasites infect the intestine of the host.

The sporonts are biassociative. The satellite is generally the larger, contrary to the general rule that either the primite is slightly the larger or the two sporonts differ but little in size. The body is elongate cylindrical, rather longer in proportion than is true of most members of the genus. The protomerite of the primite is hemispherical with no papilla or indentation at the anterior end. The constriction at the septum is shallow; the protomerite is one and one third times as broad as high and averages one sixth the total length of the sporont. The protomerite of the satellite is of practically the same width as that of the primite, but is slightly flattened. The deutomerite is elongate cylindrical, a little wider in the middle portion and tapering slightly, ending in a broadly rounded extremity. The interlocking device is not well constructed, sporonts of an association being barely contiguous and easily dissociated by slight pressure.

The body is pearl gray, and the protoplasm is not homogeneous but consists of large and small granules sparsely scattered throughout. The anterior end of the protomerite is devoid of granules. The nucleus is not visible in adults not because of the density of the protoplasm but because of the fact that the large granules seem to cling to or lie in the region of the nucleus in a cluster. The region occupied by the nucleus can, therefore, be easily detected although its outline is obscured. The nucleus is

small and spherical, containing one small karyosome. In one instance, the chromatin was arranged outside the karyosome as in the spokes of a wheel, the karyosome forming the eccentric hub. The epicyte is very thin and of even width throughout.

A table of measurements of sporonts follows; the dimensions are expressed in microns:

Total length association	368	355	310	237
Primite:				
Length protomerite	20	20	21	20
Length deutomerite	158	105	129	97
Width protomerite	35	30	30	23
Width deutomerite	75	50	57	41
Total length sporont	178	125	150	117
Ratio				
length protom.: total length	1:8.9	1:6.2	1:7.1	1:5.8
width protom.: width deutomerite	1:2.1	1:1.7	1:1.9	1:1.9
Satellite:				
Length protomerite	21	20	20	20
Length deutomerite	169	160	140	100
Width protomerite	41	35	35	32
Width deutomerite	80	75	65	45
Total length sporont	190	180	160	120
Ratio				
length protom.: total length	1:9	1:9	1:8	1:6
width protom.: width deutomerite	1:2	1:2.1	1:1.9	1:1.4

GREGARINA INTESTINALIS Watson

[Figure 168]

1915 *Gregarina intestinalis* Watson 1915:32

Host: *Pterostichus stygicus* (Say)

Location: Urbana, Illinois, November, 1914.

A dozen associations were found in the intestine of one beetle. The beetle was also infected with *Gregarina monarchia.*

The sporonts are biassociative. The body is ellipsoidal to subglobose. The protomerite of the primite is subspherical, well rounded in front, widest along the center, equal in width to one fourth to one sixth the width of the deutomerite, and one fifth the total length. There is a fairly deep constriction at the septum. The deutomerite is egg-shaped, widest about the middle portion or slightly posterior to the middle. The posterior end is broadly rounded in the primite and slightly more tapering in

the satellite. The individuals of an association are easily detached by slight pressure.

In color, this species is dark and gray, especially in the deutomerite; the protomerite is less dense. The nucleus is not visible in the live animal.

Trophozoites and cysts were not seen.

A table of measurements, in which dimensions are given in microns, follows:

Total length association	320	304		
Primite:				
Length protomerite	40	33	30	35
Length deutomerite	120	137	130	135
Width protomerite	45	42	42	55
Width deutomerite	80	80	70	82
Total length sporont	160	170	150	170
Ratio				
length protom.: total length	1:4	1:5	1:5	1:5
width protom.: width deutomerite	1:2	1:2	1:1.6	1:1.5
Satellite:				
Length protomerite	30	20		
Length deutomerite	130	114		
Width protomerite	50	32		
Width deutomerite	70	75		
Total length sporont	160	134		
Ratio				
length protom.: total length	1:5.3	1:6.7		
width protom.: width deutomerite	1:1.4	1:2.3		

GREGARINA MONARCHIA Watson

[Figure 167]

1915 *Gregarina monarchia* Watson 1915:31

Host: *Pterostichus stygicus* (Say).

Location: Urbana, Illinois, November, 1914.

Only one parasite was seen in the intestine of the host. The same beetle was infected with *Gregarina fragilis.*

The sporonts are biassociative. The body is very long and sausage shaped, easily visible to the eye. The protomerite of the primite is dome shaped, widest just below the middle portion, is but little wider than high, and in length equal to one seventh the total length of the sporont. There is a deep constriction at the septum. The deutomerite is cylindrical, of

even width throughout and but little wider than the protomerite. It is broadly rounded at the free extremity. The protomerite of the satellite is flattened top and bottom, twice as wide as high, and in length averages one sixteenth the total length of the satellite. The interlocking device between primite and satellite is deep and well developed.

The body is black, the protoplasm being very dense in all parts except the protomerite of the primite. This portion is nearly transparent except for its lower portion in which the protoplasm is dense and darkly colored. A deep groove runs crosswise just anterior to the middle portion of the protomerite and in front of it is a clear vesicular area rather indistinct in outline. The epicyte is rather thick and of the same width throughout except in the protomerite of the satellite. It is considerably thicker at the place of interlocking and a little thicker on the sides of this protomerite than elsewhere in the association. Trophozoites and cysts were not recovered. Movement of progression was not noted, but a slow contortion was evinced by a slight curving of the body.

Measurements of the one association seen are as follows, with the dimensions stated in microns:

Total length association	1070	
	Primite	Satellite
Length protomerite	80	32
Length deutomerite	490	468
Width protomerite	110	115
Width deutomerite	130	162
Total length sporont	570	500
Ratio		
length protom.: total length	1:7	1:16
width protom.: width deutomerite	1:1.2	1:1.4

GREGARINA GLOBOSA Watson

[Figure 176]

1915 *Gregarina globosa* Watson 1915:31

Host: *Coptotomus interrogatus* (Fab.).

Location: Urbana, Illinois, November, 1914.

The intestine of the host was infected; two beetles out of six examined contained two associations each.

The sporonts are biassociative. The body is subspherical, the protomerite of the primite twice as wide as high and hemispherical but rather flattened at the top. There is a constriction at the septum but it is shal-

low and scarcely noticeable in the satellite. The deutomerite is stout, three fourths as wide as long; it increases gradually in width up to the beginning of the posterior third of the body, when it becomes rapidly narrower, ending in a very broadly rounded extremity. The protomerite of the satellite is larger than that of the primite, which possibly indicates sexual dimorphism. The primite and satellite are not well interlocked.

The endocyte of the primite is dense and is not visible in vivo. The endocyte of the satellite is paler, revealing the presence of a spherical nucleus. Trophozoite and cysts were not found.

A table of measurements of one association follows in which all dimensions are given in microns:

	Primite	Satellite
Length protomerite	30	45
Length deutomerite	230	165
Width protomerite	75	110
Width deutomerite	180	155
Total length sporont	260	210
Ratio		
length protom.: total length	1:8.6	1:1.4
width protom.: width deutomerite	1:2.4	1:1.4

GREGARINA PLATYNI NOV. SPEC.

[Figures 262, 263, 264]

Host: *Platynus ruficollis* Marsh (Det. Dr. E. P. Felt).

Location: Oyster Bay, L. I., October, 1915.

The host of this species is a very small black beetle which flew in my study window one evening. Several hundred parasites were found in the intestine of the single host.

The sporonts are biassociative. They are elongate cylindrical in shape and generally lie in a slightly curved position. The largest association measured 610μ in length while sporonts averaged 300μ in length and 60μ in width. The average ratio of length protomerite : total length sporont :: 1 : 4.3 and the ratio width protomerite : width deutomerite :: 1 : 1. The protomerite is characterized by a constriction in the middle which is deep and conspicuous in sporonts of all ages and the protoplasm is much less abundant above the constriction than below. There is a deep constriction at the septum between protomerite and deutomerite. The apex of the protomerite is rounded, sometimes rather acutely while the deutomerite is cylindrical, attaining a maximum width just behind the constriction and tapering slightly in the posterior two thirds. The

extremity is bluntly rounded. The protomerite of the satellite does not show the constriction which characterizes that of the primite. It is low and flat and slightly wider than long. The constriction at the septum is not as deep here as in the primite. The attachment of the two sporonts of an association is very insecure.

The nucleus is large and spherical, often being in diameter half the width of the deutomerite. It is conspicuous in sporonts of all ages. The protoplasm is very dark in color—often black in the deutomerite but it is not as dense as that of many gregarines. It readily accumulates in masses, leaving clear spaces between. The protomerite is much less dense and tan in color; the portion above the constriction is almost devoid of protoplasm. The epimerite is spherical and very large. Myonemes are large and conspicuous, even in the adults. Movement is active. Cysts were not recovered.

A table of the more important measurements follows with dimensions expressed in microns:

Total length association	610	600	550
Primite:			
Length protomerite	70	70	60
Length deutomerite	230	230	180
Width protomerite	110	60	60
Width deutomerite	110	60	70
Total length sporont	300	300	240
Ratio			
length protom.: total length	1:4.3	1:4.3	1:4
width protom.: width deutomerite	1:1	1:1	1:1.1
Satellite:			
Length protomerite	50	40	50
Length deutomerite	260	260	260
Width protomerite	100	40	70
Width deutomerite	100	70	80
Total length sporont	310	300	310
Ratio			
length protom.: total length	1:6.2	1:7.5	1:6.2
width protom.: width deutomerite	1:1	1:1.7	1:1.1

This species is almost unique in the possession of a deep constricting groove in the protomerite of the primite. This feature, together with the long cylindrical deutomerite, readily differentiates it from other species.

UNCERTAIN SPECIES IN THE GENUS GREGARINA

GREGARINA ELATERAE Crawley

[Figure 158]

1903	*Gregarina elaterae*	Crawley	1903:46

Sporonts not seen. Crawley's description is based evidently on the cephalonts and a species can hardly be assigned to material containing no mature specimens for the cephalonts of many of the Gregarinidae are identical. Crawley's description is in part as follows:

"Epimerite spherical, protomerite elliptical, long axis perperdicular to that of deutomerite, sharp constriction at septum. Deutomerite oval to subspherical. Endocyte characteristic of cephalonts, sparse and granular. Max. length 62μ. Host *Elater* sp, larva. Taken at Wyncote, Pa."

The species is probably a member of the genus Gregarina from the epimerite, but it cannot stand as absolute. Subsequent discovery of the sporonts probably cannot be correlated with the cephalonts here described owing to a similarity of the cephalonts of so many species.

GREGARINA CURVATA (Frantzius) Diesing

1838	*Rhizinia* sp.	Hammerschmidt	1838:356
1848	*Sporadina curvata*	Frantzius	1848:195
1851	*Gregarina curvata*	Diesing	1851:14
1863	*Gregarina curvata*	Lankester	1863:94

The following and only description of the species available is quoted from Diesing:

"Proboscis ? . Receptaculum rotundatum. Corpus elongatum retrorsum attenuatum curvatum, receptaculo sexies longius. Longit. ⅛ - ¾'''."

Host: *Cetonia aurata* larv. Habitat: Intestine.

Frantzius merely names the species, giving neither drawing nor description. Diesing gives no clue as to whether the species is biassociative or not. Lankester places it in the genus Gregarina, which he characterizes by the phrase "two animals frequently hanging together" giving no description. The species has not since been mentioned in the literature, and in lieu of complete data, it is placed in the group of doubtful species under the genus Gregarina.

UNCERTAIN SPECIES OF UNCERTAIN FAMILIES

GREGARINA BOLETOPHAGI Crawley

[Figure 145]

1903 *Gregarina boletophagi* Crawley 1903-47-8

Sporonts not associative, cylindrical, 320μ in length.

"Protomerite large, variable in shape. Separated from deutomerite by a sharp constriction. Deutomerite cylindrical, with – – conical end. – – Endocyte dense, – – nucleus oval to spherical, with one karyosome. Epimerite not seen. Host: *Boletophagus cornutus*. Locality Swarthmore, Pa."

Ellis (1913b:280) says

"This species has been transferred to this genus (Anthorhynchus) from Gregarina although neither cysts nor epimerite are known, because it is not found in association and because the anterior portion of the protomerite is suggestive of the slightly produced protomerite of other species of the genus Anthorhynchus which bear epimerites. It is to be regarded as a provisional determination only."

No characteristics of the genus Anthorhynchus are evident. The epimerite, not being seen, cannot be compared with the very large globular epimerite of the latter genus and the spores cannot be compared, not being seen. The size of the species in question is only one seventh that of the type species of the genus Anthorhynchus *(A. sophiae* Schn.).

It seems that the only solution of the problem is the relegation of the species to the uncertain group.

GREGARINA MICROCEPHALA Leidy

[Figure 149]

1889 *Gregarina microcephala* Leidy 1889:11

"Body clavate, the head like a watch crystal with a little ball at the summit." Length 350μ, width 100μ, head 12μ long x 40μ wide.

Taken at Philadelphia, Pa. Host: *Arrhenoplita bicornis* Olivier *(Hoplocephalus bi.)*. Habitat: Intestine.

Ellis (1913b) corrected the host name. He left the species in the genus Gregarina. Leidy said of the species:

"It bears a close resemblance to *Echinocephalus hispidis* Schneider – – but in the one described I at no time found digitiform appendages on the head."

That the species belongs in the genus Gregarina seems doubtful; its position is left undetermined.

GREGARINA OVALIS (Crawley) Watson

[Figures 156, 157]

1903	*Hirmocystis ovalis*	Crawley	1903:50
1913	*Gregarina elaterae*	Ellis	1913b:270
1916	*Gregarina ovalis*	Watson	(This paper)

Sporonts cylindrical, 70μ long, width not given. Ratio length protomerite : total length :: 1 : 4; width protomerite : width deutomerite :: 1 : 1.1 Protomerite hemispherical, widest at base. Slight constriction at septum. Deutomerite dilated at shoulder, cylindrical, ending very bluntly. Endocyte dark brown. Anterior third of protomerite free from granules. Nucleus not seen.

Cyst and spores unknown.

Taken at Wyncote, Pa. Host: Cucujidae larva ("doubtful det."). Habitat: Intestine.

This species is probably associative but adult sporonts have not been found. The specimens illustrated are probably mature. The length is less than in most adult gregarines.

Ellis placed the species and Crawley's *Gregarina elaterae* together under the name of the latter. I have rather regarded the latter species as a doubtful one and have left this gregarine under its original name but questioning the correctness of the genus name. The species cannot be assigned to the genus Gregarina without a question of doubt arising. It is therefore placed with the uncertain species.

GREGARINA COPTOTOMI NOV. SPEC.

[Figure 172]

Host: *Coptotomus interrogatus* (Fab.). Location: Urbana, Illinois, November, 1914.

Two hosts each contained one parasite in the intestine.

The sporonts are solitary. In shape the body is elongate ellipsoidal. The protomerite is cylindrical at the base with a broadly rounded conical apex; it is as wide as high and the widest part is just anterior to the septum. There is no constriction at the septum. The deutomerite is elongate ellipsoidal broadening rapidly from the septum and soon attaining its maximum width. It remains of the same width throughout most of the length, terminating in a very broadly rounded blunt extremity. The endocyte is gray and not dense, for the nucleus is clearly

visible in vivo as an ellipsoidal body twice as long as wide and containing one large karyosome. Trophozoites and cysts have not been observed.

Measurements are as follows with dimensions given in microns:

Total length sporont	210	125
Length protomerite	30	18
Length deutomerite	180	107
Width protomerite	35	28
Width deutomerite	80	38
Ratio		
length protom.: total length	1:7	1:7
width protom.: width deutomerite	1:2.3	1:1.3
Nucleus	41 by 20	23 by 10

It is very probable that these specimens are not members of the genus Gregarina. The ellipsoidal nucleus is like that of some of the Actinocephalidae. No attempt is made to place the specimens, and they are mentioned for the completeness of the record only.

STYLOCEPHALUS sp.

[Figure 65]

?1875 *Stylocephalus longicollis* Schneider 1875: Pl. xix, fig. 2

The following description is copied from Crawley (1903:47):
"*Gregarina xylopini* Crawley.

The two gregarines shown in figures 29 and 30 are stated by Leidy to be parasites of the beetle *Xylopinus saperdioides*. Of the six beetles examined, five contained gregarines of the form shown in figure 29, one of the form shown in figure 30. These two forms are so dissimilar that it appears better, at present, to give only the figures, reserving the description until additional information is at hand."

Figure 29 is reproduced in my figure 65; figure 30 in my figure 134. The first gregarine agrees in appearance with sporonts of Schneider.

Ellis considers it as synonymous with his *Actinocephalus zophus*. I do not, however, regard it as such, but as a separate species. See discussion under *A. zophus*.

The second gregarine, (Figure 134) is evidently a specimen of *Gregarina cuneata*. The host is one of the Tenebrionidae and the drawing compares very favorably with the others listed under *G. cuneata* Stein.

GREGARINA sp. Crawley

[Figure 105]

"*Asterophora philica* Crawley. *Gregarina philica* Leidy (1889). It is impossible to give a description of this species. Figures 31 and 32 are very plainly of the same gregarine, whereas figure 33 seems almost certainly to belong to a different species. Further, the form figured by Leidy in 1889 is not so closely like that shown in figures 31 and 32 as to render it certain that the two are the same. I therefore include the three different forms under the same name, giving only the figures and reference, until such time as sufficient material is obtained to determine accurately what the actual facts may be.

The gregarines figured were about 300 microns long."

(Crawley, 1903:53).

The first two gregarines have been described under the name *Asterophora philica* (Leidy) Crawley. The third is certainly very different from the others and merits isolation. Its generic position is undetermined from lack of data and it is mentioned here simply for completeness of the record.

APPENDIX

AN UNNAMED DIDYMOPHYES FROM A JAPANESE BEETLE

In a recent article on the parasites in the intestine of a Japanese beetle, *Tribolium ferrugineum* F., (Tenebrionidae), S. Ishii (1914) has evidently confused two species of Polycystid Gregarines and designated them by the same name. He described two kinds of associations, large and small, as *Gregarina minuta*, but from his drawings and measurements the specimens are unlike. The protomerite of the primite in the first (Fig. 71) is large, subglobose, nearly flattened on the anterior surface, five eighths as wide as the deutomerite at its widest portion, and three fifths as high as wide. Its widest portion is some little distance anterior to the septum. At the septum, there is a deep constriction, the protomerite just anterior to it being wider than the deutomerite just posterior to it. In figure 143, the protomerite of the primite is smaller in proportion than in figure 71, hemispherical in shape, widest on its posterior margin, two thirds as wide as the deutomerite at its widest part, and half as high as broad. It is narrower at the septum than is the deutomerite just posterior to the septum. Thus there is a smooth, rounded contour

along the edge of the septum. The length given for the larger associations is 188μ, for the smaller 118μ.

In his general description, Ishii says "the protomerite in the satellite is not infrequently hidden from view, being entirely embedded in the deutomerite of the primite."* In his table of measurements, he says of the satellite "protomerite absent." Later he mentions "the frequent absence of protomerite in the satellite." The figure of the larger association (Fig. 71) lacks a protomerite in the satellite; the figure of the smaller (Figure 143) shows a protomerite and the table of measurements corroborates its presence.

Absence of protomerite in the satellite is not one of the diagnostic features of the genus Gregarina. If the protomerite had been absent in rare instances, the sporont might have been a "sport", but its frequent absence is, clearly enough, reason for removing the specimens from the genus Gregarina.

Absence of the protomerite of the satellite is the chief diagnostic character of the family Didymophyidae, in which there is but one genus, Didymophyes, and of this family only. Therefore this polycystid gregarine which lacks a protomerite in the satellite belongs to the latter genus and I have (p. 133) designated it *Didymophyes minuta* (Ishii). Of course, the determination cannot be absolute without the spores and epimerite, but if the specimens belong to any known genus, they must belong to the genus Didymophyes.

Of the four hitherto described species in this genus, two have been recovered from Coleoptera. The present species is the smallest to be recorded, by 67μ. (*D. longissima* Sieb.).

The smaller associations which Ishii described and in which the protomerite of the satellite is present, belong, without doubt, to the genus Gregarina, and the name *G. minuta* refers to them only.

There is also either a confusion of species or an error in observation in regard to the species *Gregarina crassa* (Ishii, 1914:438). He illustrates but one specimen and, in this one indistinct figure, it is impossible to determine whether or not there is a protomerite in the satellite. Since only one specimen is measured and but one drawn, no comparisons can be made between the specimens with and those without protomerites in the satellites and I am unable to determine the number of species under consideration and the systematic position of the specimen described.

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*This statement is construed to mean that the author did not see the protomerite of the satellite and inferred that it was embedded in the deutomerite of the primite.

PART IV

THE CEPHALINE GREGARINES OF THE WORLD

TOGETHER WITH THEIR HOSTS

Parasite	Host	Order or Class
DIDYMOPHYIDAE		
Didymophyes gigantea	*Oryctes nasicornis* (L.)	Coleoptera
	Oryctes sp.	
	Phyllognathus sp.	
leuckarti	*Aphodius prodromus* (Brahm.)	Coleoptera
	Aphodius nitidulus F.	
longissima	*Gammarus pulex* (L.)	Crustacea
	Orchestia littorea Leach	
minuta	*Tribolium ferrugineum* F.	Coleoptera
paradoxa	*Geotrupes stercorarius* (L.)	Coleoptera
GREGARINIDAE		
Gregarina achetaeabbreviatae	*Gryllus abbreviatus* Serv.	Orthoptera
acridiorum	*Pamphagus* sp.	
	Tryxalis sp.	
	Sphingonotus sp.	Orthoptera
acuta	*Trox perlatus* Scriba	Coleoptera
amarae	*Poecilus cupreus* (L.)	Coleoptera
barbarara	*Coccinella* sp.	Coleoptera
blattarum	*Periplaneta americana* (L.)	Orthoptera
	Periplaneta orientalis (L.)	Orthoptera
	Blattella germanica (L.)	Orthoptera
boletophagi	*Boletophagus cornutus* Panz.	Coleoptera
cavalierina	*Dendarus tristis* Rossi	Coleoptera
clausi	*Phronima* sp.	Crustacea
conica	Coleoptera and Orthoptera	
consobrina	*Ceuthophilus valgus* Scud.	Orthoptera
coptotomi	*Coptotomus interrogatus* (Fab.)	Coleoptera
cuneata	*Tenebrio molitor* L.	Coleoptera
curvata	*Cetonia aurata* L.	Coleoptera
davini	*Gryllomorpha dalmatina* Ocsk.	Orthoptera
elaterae	*Elater* sp.	Coleoptera
elongata	*Crypticus* sp.	Coleoptera
ensiformis	*Salpa aeruginosa*	Tunicata
flava	*Salpa confoederata*	Tunicata
	Salpa vagina	Tunicata
fragilis	*Coccinella* sp.	Coleoptera
galliveri	*Gryllus abbreviatus* Serv.	Orthoptera
gammari	*Gammarus* sp.	Crustacea
globosa	*Coptotomus interrogatus* (Fab.)	Coleoptera

Parasite	Host	Order or Class
gracilis	*Elater* sp.	Coleoptera
granulosa	*Ephemera* sp.	Neuroptera
grisea	*Tenebrio castaneus* Knoch	Coleoptera
guatemalensis	*Ninus interstitialis* Esch.	Coleoptera
hyalocephala	*Tridactylus variegatus* Latr.	Orthoptera
illinensis	*Ischnoptera pennsylvanica* (deGeer)	Orthoptera
intestinalis	*Pterostichus stygicus* (Say)	Coleoptera
katherina	*Coccinella novemnotata* Herbst	Coleoptera
kingi	*Gryllus abbreviatus* Serv.	Orthoptera
lagenoides	*Lepisma saccharina* L.	Thysanura
laucournetensis	*Parnus* sp.	Coleoptera
locustae	*Dissosteira carolina* L.	Orthoptera
longa	*Tipula* sp.	Diptera
longiducta	*Ceuthophilus maculatus* (Say)	Orthoptera
	Ceuthophilus latens Scud.	Orthoptera
longirostris	*Thanasinius formicarius* (L.)	Coleoptera
lucani	*Lucanus dama* Thunb.	Coleoptera
macrocephala	*Nemobius sylvestris* (F.)	Orthoptera
	Gryllus domesticus L.	Orthoptera
marteli	*Embia* sp.	Neuroptera
melolonthae	*Melolontha brunnea* Blanch.	Coleoptera
microcephala	*Arrhenoplita bicornis* Oliv.	Coleoptera
millaria	*Gammarus* sp.	Crustacea
	Astacus sp.	Crustacea
minuta	*Tribolium ferrugineum* F.	Coleoptera
monarchia	*Pterostichus stygicus* (Say)	Coleoptera
munieri	*Timarcha tenebricosa* (F.)	Coleoptera
	Chrysomela violacea (Goeze)	Coleoptera
	Chrysomela haemoptera L.	Coleoptera
mystacidorum	*Mystacida* sp.	Neuroptera
nereidis denticulata	?	Annelida
nigra	Acridiidae	Orthoptera
oblonga	*Oedipoda migratoria* L.	Orthoptera
	Oedipoda stridula L.	
	Gryllus campestris L.	Orthoptera
ovalis	Cucujidae	Coleoptera
ovata	*Forficula auricularia* L.	Orthoptera
oviceps	*Gryllus abbreviatus* Serv.	Orthoptera
	Gryllus americanus Blatch.	
panchlorae	*Panchlora exoleta* Klug	Orthoptera
paranensis	*Schistocerca paranensis* Burm.	Orthoptera
parva	*Harpalus caliginous* Fab.	Coleoptera
	Harpalus pennsylvanicus Dej.	
passali	*Passalus cornutus* Fab.	Coleoptera

Parasite	Host	Order or Class
platyni	*Platynus ruficollis* Marsh	Coleoptera
podurae	*Orchesella villosa*	Thysanura
polymorpha	*Tenebrio molitor* L.	Coleoptera
praemorsa	*Platycarcinus* sp.	Crustacea
psocorum	*Psocus* sp.	Neuroptera
pterotracheae	*Pterotrachea* sp.	Mollusca
rigida	Acridiidae	Orthoptera
salpae	*Salpa maxima*	Tunicata
scarabaei	*Scarabaeus relictus*	Coleoptera
serpentula	*Periplaneta orientalis* (L.)	Orthoptera
socialis	*Eryx ater* Fab.	Coleoptera
soror	uncertain	Coleoptera
sphaerulosa	*Gryllotalpa* sp.	Locustidae
statirae	*Statira unicolor* Blanch.	Coleoptera
steini	*Tenebrio molitor* L.	Coleoptera
stygia	*Ceuthophilus stygius* (Scud.)	Orthoptera
tenebrionella	Tenebrionidae	Coleoptera
tenuis	*Allecula* sp.	Coleoptera
termitis	*Termes* sp.	Neuroptera
tipula	*Tipula* sp.	Diptera
udeopsyllae	*Udeopsylla nigra*	Locustidae
valettei	*Pollicipes* sp.	Crustacea
sp. (Bolsius)	*Glossiphonia* sp.	Annelida
	Herpobdella sp.	
sp. (Crawley)	*Nyctobates pennsylvanica* (deGeer)	Coleoptera
sp. (Gaede)	*Blaps mortisaga* L.	Coleoptera
sp. (Hallez)	*Dendrocoelum lacteum*	Platyhelminthes
sp. (Kölliker)	*Balanus* sp.	Crustacea
sp. (Mawrodiadi)	*Balanus* sp.	Crustacea
sp. (Moseley)	*Peripatus* sp.	Onycophora
sp. (Pfeiffer)	*Gammarus pulex*	Crustacea
sp. (Porter)	*Rhynchobolus americanus*	Annelida
sp. (Ritter)	*Perophora annectens*	Tunicata
sp. (Solger)	*Balanus improvisus*	Crustacea
Hirmocystis asidae	*Asida servillei* Sol.	Coleoptera
gryllotalpae	*Gryllotalpa gryllotalpa* (L.)	Orthoptera
harpali	*Harpalus pennsylvanicus erythropus* (Dej.)	Coleoptera
polymorpha	*Limnobia* sp.	Diptera
ventricosa	*Tipula* sp.	Diptera
	Pachyrhina sp.	Diptera
Sphaerocystis simplex	*Cyphon pallidulus* Boh.	Coleoptera
Hyalospora affinis	*Machilis cylindrica* Geoff.	Thysanura
reduvii	*Reduvius personatus* L.	Hemiptera

Parasite	Host	Order or Class
roscoviana	*Perobius maritimus* Leach	Thysanura
Cnemidospora lutea	*Glomeris* sp.	Myriapoda
Euspora fallax	*Rhizotrogus aestivus* Oliv.	Coleoptera
Gamocystis ephemerae	*Ephemera* sp.	Neuroptera
tenax	*Blattella lapponica* L.	Orthoptera
Frenzelina chtamali	*Chtamalus stellatus*	Crustacea
conformis	*Pachygraspus marmoratus*	Crustacea
delphinia	*Talorchestia longicornis*	Crustacea
dromiae	*Dromia dromia*	Crustacea
fossor	*Pinnotheres pisum*	Crustacea
nigrofusca	*Uca pugnax* and *Uca pugilator*	Crustacea
ocellata	*Eupagurus prideauxi*	Crustacea
olivia	*Libinia dubia*	Crustacea
portunidarum	*Portunus arcuatus*	Crustacea
praemorsa	*Cancer pagurus*	Crustacea
Uradiophora communis	*Balanus* sp.	Crustacea
cuenoti	*Atyaephyra desmaresti*	Crustacea
Leidyana erratica	*Gryllus abbreviatus* Serv.	Orthoptera
	Gryllus pennsylvanicus Burm.	
gryllorum	*Gryllus domesticus* (L.)	Orthoptera
DACTYLOPHORIDAE		
Dactylophorus robustus	*Cryptops hortensis* Leach	Myriapoda
	Cryptops anomalons lusitanus Verh.	
Nina giardi	*Scolopendra oraniensis*	Myriapoda
giardi corsicum	*Scolopendra oraniensis lusitanica* Verh.	Myriapoda
gracilis	*Scolopendra cingulata* (Latr.)	Myriapoda
indicia	*Scolopendra subspinipes* Leach	Myriapoda
Trichorhynchus pulcher	*Scutigera* sp.	Myriapoda
	Scutigera forceps (Raf.)	Myriapoda
Echinomera hispida	*Lithobius forficatus* Linn.	Myriapoda
	Lithobius coloradensis Cock.	Myriapoda
horrida	*Lithobius calcaratus* Koch	Myriapoda
Rhopalonia geophili	*Himantarium gabrielis* Linn.	Myriapoda
	Stigmatogaster gracilis Mein.	Myriapoda
stella	*Himantarium gabrielis* Linn.	Myriapoda
Acutispora macrocephala	*Lithobius forficatus* Linn.	Myriapoda
Metamera schubergi	*Hirudinea* sp.	Annelida
ACTINOCEPHALIDAE		
Actinocephalus acutispora	*Silpha laevigata* F.	Coleoptera
americanus	*Galerita bicolor* Drury	Coleoptera
brachydactylus	*Aeshna* sp.	Neuroptera
caudatus	*Sciara* sp.	Diptera
conicus	*Dorcus parallelopipedus* (L.)	Coleoptera

Parasite	Host	Order or Class
crassus	*Leptochirus edax* Sharp	Coleoptera
dicaeli	*Dicaelus ovalis* Lec.	Coleoptera
digitatus	*Chlaenius vestitus* (Payk.)	Coleoptera
dujardini	*Lithobius forficatus* L.	Myriapoda
dytiscorum	*Dytiscus* sp.	Coleoptera
fimbriatus	*Dissosteira carolina* L.	Coleoptera
gimbeli	*Harpalus pennsylvanicus* Dej.	Coleoptera
harpali	*Harpalus caliginosus* Fab.	Coleoptera
octacanthus	*Phryganea* sp.	Neuroptera
repelini	*Phalangium* sp.	Arachnida
sieboldi	*Agrion* sp.	Neuroptera
stelliformis	*Ocypus olens* (Mull.)	Coleoptera
	Carabus auratus L.	Coleoptera
	Carabus violaceus L.	
	Rhizotrogus sp.	
striatus	*Scolopendra cingulata* (Latr.)	Myriapoda
tipulae	*Tipula* sp.	Diptera
zophus	*Nyctobates barbata* Knoch	Coleoptera
	Nyctobates pennsylvanica (deGeer)	Coleoptera
sp.	*Ctenophora* sp.	Diptera
Geniorhynchus aeschna	*Aeschna constricta* Say	Neuroptera
monnieri	*Libellules* sp.	Neuroptera
Phialoides ornator	*Hydrophilus piceus* (L.)	Coleoptera
Pyxinia crystalligera	*Dermestes vulpinus* Fabr.	Coleoptera
	Dermestes peruvianus Casteln.	
frenzeli	*Attagenus pellio* L.	Coleoptera
möbuszi	*Anthrenus verbasci* Oliv.	Coleoptera
rubecula	*Dermestes lardarius* L.	Coleoptera
	Dermestes vulpinus Fabr.	Coleoptera
Beloides firmus	*Dermestes lardarius* L.	Coleoptera
tenuis	*Dermestes undulatus* Brahm.	Coleoptera
Legeria agilis	*Colymbetes* sp.	Coleoptera
Coleorhynchus heros	*Nepa* sp.	Hemiptera
Bothriopsis histrio	*Dytiscus* sp.	Coleoptera
	Hydaticus cinereus L.	
	Colymbetes fuscus L.	
	Acilius sulcatus L.	
terpsichorella	*Hydrophilus* sp.	Coleoptera
Asterophora cratoparis	*Cratoparis lunatus* Fab.	Neuroptera
elegans	*Phryganea* sp.	Neuroptera
mucronata	*Rhyacophila* sp.	Neuroptera
philica	*Nyctobates pennsylvanica* (deGeer)	Coleoptera
Schneideria mucronata	*Bibio* sp.	Diptera
Stictospora provincialis	*Melolontha* sp.	Coleoptera
	Rhizotrogus sp.	

Parasite	Host	Order or Class
Stylocystis ensifera	*Leptochirus edax* Sh.	Coleoptera
praecox	*Tanypus* sp.	Diptera
Steinina harpali	*Harpalus pennsylvanicus longior* (Kirby)	Coleoptera
obconica	*Tribolium ferrugineum* F.	Coleoptera
ovalis	*Tenebrio molitor* L.	Coleoptera
rotunda	*Amara angustata* Say	Coleoptera
Taeniocystis truncata	*Sericostoma*	Neuroptera
Amphoroides calverti	*Callipus lactarius* (Say)	Myriapoda
	Lysiopetalum lactarium (Say)	Myriapoda
polydesmi	*Polydesmus complanatus* (L.)	Myriapoda
	Polydesmus dispar Silvestri	Myriapoda
Pileocephalus bergi	*Necrobia ruficollis* Fabr.	Coleoptera
blaberae	*Blabera claraziana* Sauss.	Orthoptera
chinensis	*Mystacides* sp.	Neuroptera
Anthorhynchus sophiae	*Phalangida* sp.	Arachnida
fissidens	*Phalangides* sp.	Arachnida
goronowitschi	*Phalangium* sp.	Arachnida
Sciadophora phalangii	*Phalangium* sp.	Arachnida
Hoplorhynchus actinotus	*Scolopocryptops sexspinosus* (Say)	Myriapoda
	Scolopocryptops sp.	
scolopendras	*Scolopendra woodi* Mein.	Myriapoda
Amphorocephalus amphorellus	*Scolopendra heros* Giard	Myriapoda
ACANTHOSPORIDAE		
Acanthospora pileata	*Omoplus* sp.	Coleoptera
	Cistelides sp.	Neuroptera
polymorpha	*Hydrous caraboides* (L.)	Coleoptera
Corycella armata	*Gyrinus natator* (L.)	Coleoptera
Ancyrophora gracilis	*Carabus* sp.	Coleoptera
	Carabus auratus L.	
	Carabus violaceus L.	
	Silpha thoracica L.	Coleoptera
uncinata	*Dytiscus* sp.	Coleoptera
	Colymbetes sp.	
	Sericostoma sp.	
	Limnophilus rhombicus (L.)	Neuroptera
Cometoides capitatus	*Hydrous* sp.	Coleoptera
crinitus	*Hydrobius* sp.	Coleoptera
MENOSPORIDAE		
Menospora polyacantha	*Agrion* sp.	Neuroptera
STYLOCEPHALIDAE		
Stylocephalus balani	*Balanus* sp.	Crustacea
brevirostris	*Hydrophilus* sp.	Coleoptera
caudatus	*Phalangides* sp.	Arachnida
giganteus	*Eleodes* sp.	Coleoptera
	Eusattus sp.	

Parasite	Host	Order or Class
	Asida opaca Say	
	Asida sp.	Coleoptera
gladiator	*Helenophorus collaris* L.	Coleoptera
heeri	*Phryganea* sp.	Neuroptera
longicollis	*Blaps mortisaga* L.	Coleoptera
oblongatus	*Opatrum sabulosum* (L.)	Coleoptera
	Asida grisea (F.)	
oligacanthus	*Agrion* sp.	Neuroptera
phallusiae	*Phallusia* sp.	Mollusca
sp.	*Xylopinus saperdioides* Oliv.	Coleoptera
Sphaerorhynchus ophioides	*Acis* sp.	Coleoptera
Lophocephalus insignis	*Helops striatus* Geoff.	Coleoptera
Cystocephalus algerianus	*Pimelia* sp.	Coleoptera
Oocephalus hispanus	*Morica* sp.	Coleoptera
STENOPHORIDAE		
Stenophora aculeata	*Craspedosoma rawlinsii* Verh.	Myriapoda
brölemanni	*Blaniulus hirsutus* Bröl.	Myriapoda
	Brachyiulus superus Latzel	Myriapoda
	Brachyiulus pusillus lusitanus Verh.	Myriapoda
chordeume	*Chordeuma silvestre* C. Koch	Myriapoda
cockerellae	*Parajulus* sp.	Myriapoda
corsica	*Craspedosoma legeri* Bröl.	Myriapoda
dauphinia	*Julus mediterraneus* Latzel	Myriapoda
	Julus boleti C. Koch	Myriapoda
	Julus fallax Meinert	Myriapoda
diplocorpa	*Euryurus erythropygus* (Brandt)	Myriapoda
elongata	*Orthomorpha coarctata* (Sauss.)	Myriapoda
fontariae	*Polydesmus* sp.	Myriapoda
	Fontaria sp.	Myriapoda
impressa	*Parajulus impressus* (Say)	Myriapoda
juli	*Julus sabulosus* (L.)	Myriapoda
	Julus fallax Mein.	Myriapoda
julipusilli	*Julus* and *Parajulus*	Myriapoda
lactaria	*Callipus lactarius* (Say)	Myriapoda
larvata	*Spirobolus spinigerus* Wood	Myriapoda
nematoides	*Strongylosoma italicum* Latz.	Myriapoda
polydesmi	*Fontaria virginiensis* (Drury)	Myriapoda
polyxeni	*Polyxenus lagurus* (L).	Myriapoda
producta	*Julus varius* Fabricius	Myriapoda
robusta	*Parajulus venustus* Wood	Myriapoda
	Orthomorpha gracilis (C. Koch)	Myriapoda
	Orthomorpha sp.	Myriapoda
silene	*Lysiopetalum foetidissimum* Sav.	Myriapoda
spiroboli	*Spirobolus* sp.	Myriapoda
varians	*Schizophyllum corsicum* Bröl.	

GENERA OF UNCERTAIN POSITION

Ulivina elliptica	*Audouinia* sp.	Annelida
Ganymedes anaspidis	*Anaspides* sp.	Crustacea
Nematoides fusiformis	*Balanus* sp.	Crustacea
Agrippina bona	*Ceratophyllus fasciatus* Bosk.	Arachnida

HOSTS WITH THEIR CEPHALINE GREGARINE PARASITES

Host	Group	Parasite
Acilius sulcatus L.	Coleoptera	*Bothriopsis histrio*
Acis sp.	Coleoptera	*Sphaerorhynchus ophioides*
Aeschna constricta Say	Neuroptera	*Geniorhynchus aeschna*
sp.	Neuroptera	*Actinocephalus brachydactylus*
Agrion sp.	Neuroptera	*Menospora polyancatha*
sp.	Neuroptera	*Actinocephalus sieboldi*
sp.	Neuroptera	*Stylocephalus oligacanthus*
Allecula sp.	Coleoptera	*Gregarina tenuis*
Alobates pennsylvanica deGeer	Coleoptera	*Actinocephalus zophus*
Amara angustata Say	Coleoptera	*Steinina rotunda*
Anaspides sp.	Crustacea	*Ganymedes anaspidis*
Anthrenus verbasci Oliv.	Coleoptera	*Pyxinia möbuszi*
Aphodius nitidulus F.	Coleoptera	*Didymophyes leuckarti*
prodromus (Brahm.)	Coleoptera	*Didymophyes leuckarti*
Arrhenoplita bicornis Oliv.	Coleoptera	*Gregarina microcephala*
Asida grisea (F.)	Coleoptera	*Stylocephalus oblongatus*
opaca Say	Coleoptera	*Stylocephalus giganteus*
servillei Sol.	Coleoptera	*Hirmocystis asidae*
sp.	Coleoptera	*Stylocephalus giganteus*
Astacus sp.	Crustacea	*Gregarina millaria*
Attagenus pellio L.	Coleoptera	*Pyxinia frenzeli*
Atyaephyra desmaresti	Crustacea	*Uradiophora cuenoti*
Audouinia sp.	Annelida	*Ulivina elliptica*
Balanus improvisus	Crustacea	*Gregarina* sp. (Solger)
sp.	Crustacea	*Gregarina* sp. (Mawrodiadi)
sp.	Crustacea	*Gregarina* sp. (Kölliker)
sp.	Crustacea	*Uradiophora communis*
sp.	Crustacea	*Stylocephalus balani*
sp.	Crustacea	*Nematoides fusiformis*
Bibio sp.	Diptera	*Schneideria mucronata*
Blabera claraziana Sauss.	Orthoptera	*Pileocephalus blaberae*
Blaniulus hirsutus Bröl.	Myriapoda	*Stenophora brölemanni*
Blaps mortisaga L.	Coleoptera	*Stylocephalus longicollis*
		Gregarina sp. (Gaede)
Blattella germanica (L.)	Orthoptera	*Gregarina blattarum*
lapponica L.	Orthoptera	*Gamocystis tenax*
Boletophagus cornutus Panz.	Coleoptera	*Gregarina boletophagi*

Host	Group	Parasite
Brachyiulus superus Latz.	Myriapoda	*Stenophora brölemanni*
pusillus lusitanus Verh.	Myriapoda	*Stenophora brölemanni*
Brachystola magna Giard	Orthoptera	*Gregarina rigida*
Callipus lactarius (Say)	Myriapoda	*Amphoroides calverti*
		Stenophora lactaria
Cancer pagurus	Crustacea	*Frenzelina praemorsa*
Carabus auratus L.	Coleoptera	*Actinocephalus stelliformis*
		Ancyrophora gracilis
violaceus L.	Coleoptera	*Actinocephalus stelliformis*
		Ancyrophora gracilis
sp.	Coleoptera	*Ancyrophora gracilis*
Ceratophyllus fasciatus Bosk.	Arachnida	*Agrippina bona*
Cetonia aurata L.	Coleoptera	*Gregarina curvata*
Ceuthophilus latens Scud.	Orthoptera	*Gregarina longiducta*
maculatus (Say)	Orthoptera	*Gregarina longiducta*
stygius (Scud.)	Orthoptera	*Gregarina stygia*
valgus Scud.	Orthoptera	*Gregarina consobrina*
Chlaenius vestitus (Payk.)	Coleoptera	*Actinocephalus digitatus*
Chordeuma silvestre C. Koch	Myriapoda	*Stenophora chordeume*
Chrysomela haemoptera L.	Coleoptera	*Gregarina munieri*
violacea (Goeze)	Coleoptera	*Gregarina munieri*
Chtamalus stellatus	Crustacea	*Frenzelina chtamali*
Cistelides sp.	Neuroptera	*Acanthospora pileata*
Coccinella novemnotata Herbst	Coleoptera	*Gregarina katherina*
Coccinella sp.	Coleoptera	*Gregarina barbarara*
sp.	Coleoptera	*Gregarina fragilis*
Colymbetes fuscus L.	Coleoptera	*Bothriopsis histrio*
sp.	Coleoptera	*Legeria agilis*
sp.	Coleoptera	*Ancyrophora uncinata*
Coptotomus interrogatus (Fab.)	Coleoptera	*Gregarina globosa*
		Gregarina coptotomi
Craspedosoma legeri	Myriapoda	*Stenophora corsica*
rawlinsii Verh.	Myriapoda	*Stenophora aculeata*
Cratoparis lunatus Fab.	Coleoptera	*Asterophora craptoparis*
Crypticus sp.	Coleoptera	*Gregarina elongata*
Cryptops anomalons lusitanus Verh.	Myriapoda	*Nina gracilis*
hortensis Leach	Myriapoda	*Dactylophorus robustus*
Ctenophora sp.	Diptera	*Actinocephalus* sp.
Cyphon pallidulus Boh.	Coleoptera	*Sphaerocystis simplex*
Dendarus tristis Rossi	Coleoptera	*Gregarina cavalierina*
Dendrocoelum lacteum	Platyhelminthes	*Gregarina* sp. (Hallez)
Dermestes lardarius L.	Coleoptera	*Beloides firmus*
		Pyxinia rubecula
peruvianus Casteln.	Coleoptera	*Pyxinia crystalligera*

Host	Group	Parasite
undulatus Brahm.	Coleoptera	*Beloides tenuis*
vulpinus Fabr.	Coleoptera	*Pyxinia crystalligera*
		Pyxinia rubecula
Dicaelus ovalis Lec.	Coleoptera	*Actinocephalus dicaeli*
Dissosteira carolina L.	Orthoptera	*Gregarina locustae*
		Actinocephalus fimbriatus
Dorcus parallelopipedus L.	Coleoptera	*Actinocephalus conicus*
Dromia dromia	Crustacea	*Frenzelina dromiae*
Dytiscus sp.	Coleoptera	*Actinocephalus dytiscorum*
sp.	Coleoptera	*Bothriopsis histrio*
sp.	Coleoptera	*Ancyrophora uncinata*
Elater sp.	Coleoptera	*Gregarina elaterae*
sp.	Coleoptera	*Gregarina gracilis*
Eleodes sp.	Coleoptera	*Stylocephalus giganteus*
Embia sp.	Neuroptera	*Gregarina marteli*
Encoptolophus sordidus (Burm.)	Orthoptera	*Gregarina rigida*
		Gregarina nigra
Ephemera sp.	Neuroptera	*Gamocystis ephemerae*
sp.	Neuroptera	*Gregarina granulosa*
Eryx ater Fab.	Coleoptera	*Gregarina socialis*
Eupagurus prideauxi	Crustacea	*Frenzelina ocellata*
Euryurus erythropygus (Brandt)	Myriapoda	*Stenophora diplocorpa*
Eusattus sp.	Coleoptera	*Stylocephalus giganteus*
Fontaria sp.	Myriapoda	*Stenophora fontariae*
virginiensis (Drury)	Myriapoda	*Stenophora polydesmi*
Forficula auricularia L.	Orthoptera	*Gregarina ovata*
Galerita bicolor Drury	Coleoptera	*Actinocephalus americanus*
Gammarus pulex (L.)	Crustacea	*Didymophyes longissima*
		Gregarina sp. (Pfeiffer)
sp.	Crustacea	*Gregarina gammari*
sp.	Crustacea	*Gregarina millaria*
Geotrupes stercorarius (L.)	Coleoptera	*Didymophyes paradoxa*
Glomeris sp.	Myriapoda	*Cnemidospora lutea*
Glossiphonia sp.	Annelida	*Gregarina* sp. (Bolsius)
Gryllomorpha dalmatina Ocsk.	Orthoptera	*Gregarina davini*
Gryllotalpa gryllotalpa (L.)	Orthoptera	*Hirmocystis gryllotalpae*
sp.		*Gregarina sphaerulosa*
Gryllus abbreviatus Serv.	Orthoptera	*Gregarina achetaeabbreviatae*
		Gregarina galliveri
		Gregarina kingi
		Gregarina oviceps
		Leidyana erratica
campestris L.	Orthoptera	*Gregarina oblonga*
domesticus L.	Orthoptera	*Gregarina macrocephala*
		Leidyana gryllorum

Host	Group	Parasite
pennsylvanicus Burm.	Orthoptera	*Leidyana erratica*
Gyrinus natator (L.)	Coleoptera	*Corycella armata*
Harpalus caliginosus Fab.	Coleoptera	*Actinocephalus harpali*
		Gregarina parva
		Hirmocystis harpali
Harpalus pennsylvanicus Dej.	Coleoptera	*Actinocephalus gimbeli*
		Gregarina parva
pennsylvanicus longior (Kirby)	Coleoptera	*Steinina harpali*
Helenophorus collaris L.	Coleoptera	*Stylocephalus gladiator*
Helops striatus Geoff.	Coleoptera	*Lophocephalus insignis*
Herpobdella sp.	Annelida	*Gregarina* sp. (Bolsius)
Hesperotettix pratensis Scudd.	Orthoptera	*Gregarina rigida*
Himantarium gabrielis Linn.	Myriapoda	*Rhopalonia geophili*
		Rhopalonia stella
Hirudinea sp.	Annelida	*Metamera schubergi*
Hydaticus cinereus L.	Coleoptera	*Bothriopsis histrio*
Hydrobius sp.	Coleoptera	*Cometoides crinitus*
Hydrophilus piceus (L.)	Coleoptera	*Phialoides ornata*
sp.	Coleoptera	*Stylocephalus brevirostris*
sp.	Coleoptera	*Bothriopsis terpsichorella*
Hydrous caraboides (L.)	Coleoptera	*Acanthospora polymorpha*
sp.	Coleoptera	*Cometoides capitatus*
Ischnoptera pennsylvanica (deGeer)	Orthoptera	*Gregarina illinensis*
Julus boleti C. Koch.	Myriapoda	*Stenophora dauphinia*
		Stenophora juli
fallax Mein.	Myriapoda	*Stenophora dauphinia*
		Stenophora juli
mediterraneus Latz.	Myriapoda	*Stenophora dauphinia*
sabulosus (L.)	Myriapoda	*Stenophora juli*
varius Fab.	Myriapoda	*Stenophora producta*
sp.	Myriapoda	*Stenophora julipusilli*
Lepisma saccharina L.	Thysanura	*Gregarina lagenoides*
Leptochirus edax Sharp	Coleoptera	*Actinocephalus crassus*
		Stylocystis ensifera
Libellules sp.	Neuroptera	*Geniorhynchus monnieri*
Libinia dubia	Crustacea	*Frenzelina olivia*
Limnobia sp.	Diptera	*Hirmocystis polymorpha*
Limnophilus rhombicus	Neuroptera	*Ancyrophora uncinata*
Lithobius calcaratus Koch	Myriapoda	*Echinomera horrida*
coloradensis Cock.	Myriapoda	*Echinomera hispida*
forficatus Linn.	Myriapoda	*Actinocephalus dujardini*
		Acutispora macrocephala
		Echinomera hispida

Host	Group	Parasite
Lucanus dama Thunb.	Coleoptera	*Gregarina lucani*
Lysiopetalum foetidissimum Sav.	Myriapoda	*Stenophora silene*
lactarium (Say)	Myriapoda	*Amphoroides calverti*
Machilis cylindrica Geoff.	Thysanura	*Hyalospora affinis*
Melolontha brunnea Blanch.	Coleoptera	*Gregarina melolonthae*
sp.	Coleoptera	*Stictospora provincialis*
Melanoplus angustipennis (Dodge)	Orthoptera	*Gregarina rigida*
atlantis (Riley)		*Gregarina rigida*
bivittatus (Say)		*Gregarina rigida*
coloradensis (Say)		*Gregarina rigida*
differentialis (Uhler)		*Gregarina rigida*
femoratus (Burm.)		*Gregarina rigida*
femur-rubrum (deGeer)		*Gregarina rigida*
luridus (Dodge)		*Gregarina nigra*
Morica sp.	Coleoptera	*Oocephalus hispanus*
Mystacida sp.	Neuroptera	*Gregarina mystacidorum*
Mystacides sp.	Neuroptera	*Pileocephalus chinensis*
Necrobia ruficollis Fabr.	Coleoptera	*Pileocephalus bergi*
Nemobius sylvestris (F.)	Orthoptera	*Gregarina macrocephala*
Nepa sp.	Hemiptera	*Coleorhynchus heros*
Ninus interstitialis Esch.	Coleoptera	*Gregarina guatemalensis*
Nyctobates barbata Knoch	Coleoptera	*Actinocephalus zophus*
pennsylvanica (deGeer)	Coleoptera	*Actinocephalus zophus*
		Asterophora philica
		Gregarina sp. (Crawley)
Ocypus olens (Mull.)	Coleoptera	*Actinocephalus stelliformis*
Oedipoda migratoria L.	Orthoptera	*Gregarina oblonga*
stridula L.	Orthoptera	*Gregarina oblonga*
Omoplus sp.	Coleoptera	*Acanthospora pileata*
Opatrum sabulosum (L.)	Coleoptera	*Stylocephalus oblongatus*
Orchesella villosa	Thysanura	*Gregarina podurae*
Orchestia littorea Leach	Crustacea	*Didymophyes longissima*
Orthomorpha coarctata (Sauss.)	Myriapoda	*Stenophora elongata*
gracilis (C. Koch)	Myriapoda	*Stenophora robusta*
sp.	Myriapoda	*Stenophora robusta*
Oryctes nasicornis (L.)	Coleoptera	*Didymophyes gigantea*
sp.	Coleoptera	*Didymophyes gigantea*
Pachygraspus marmoratus	Crustacea	*Frenzelina conformis*
Pachyrhina sp.	Diptera	*Hirmocystis ventricosa*
Pamphagus sp.	Orthoptera	*Gregarina acridiorum*
Panchlora exoleta (Klug)	Orthoptera	*Gregarina panchlorae*

Host	Group	Parasite
Parajulus impressus (Say)	Myriapoda	*Stenophora impressa*
venustus Wood	Myriapoda	*Stenophora robusta*
sp.	Myriapoda	*Stenophora cockerellae*
sp.	Myriapoda	*Stenophora julipusilli*
Parnus sp.	Coleoptera	*Gregarina laucournetensis*
Passalus cornutus Fab.	Coleoptera	*Gregarina passali*
Periplaneta americana (L.)	Orthoptera	*Gregarina blattarum*
orientalis (L.)	Orthoptera	*Gregarina blattarum*
		Gregarina serpentula
Peripatus sp.	Onycophora	*Gregarina* sp. (Moseley)
Perophora annectens	Tunicata	*Gregarina* sp. (Ritter)
Petrobius maritimus Leach	Thysanura	*Hyalospora roscoviana*
Phalangida sp.	Arachnida	*Anthorhynchus sophiae*
Phalangides sp.	Arachnida	*Anthorhynchus fissidens*
sp.	Arachnida	*Stylocephalus caudatus*
Phalangium sp.	Arachnida	*Anthorhynchus gonorowitschi*
sp.	Arachnida	*Sciadophora phalangii*
sp.	Arachnida	*Actinocephalus repelini*
Phallusia sp.	Mollusca	*Stylocephalus phallusiae*
Phronima sp.	Crustacea	*Gregarina clausi*
Phryganea sp.	Neuroptera	*Actinocephalus octacanthus*
sp.	Neuroptera	*Asterophora elegans*
sp.	Neuroptera	*Stylocephalus heeri*
Phyllognathus sp.	Coleoptera	*Didymophyes gigantea*
Pimelia sp.	Coleoptera	*Cystocephalus algerianus*
Pinotheres pisum	Crustacea	*Frenzelina fossor*
Platycarcinus sp.	Crustacea	*Gregarina praemorsa*
Platynus ruficollis Marsh.	Coleoptera	*Gregarina platyni*
Poecilus cupreus (L.)	Coleoptera	*Gregarina amarae*
Pollicipes sp.	Crustacea	*Gregarina valettei*
Polydesmus complanatus (L.)	Myriapoda	*Amphoroides polydesmi*
dispar Silvestri	Myriapoda	*Amphoroides polydesmi*
sp.	Myriapoda	*Stenophora fontariae*
Polyxenus lagurus (L.)	Myriapoda	*Stenophora polyxeni*
Portunus arcuatus	Crustacea	*Frenzelina portunidarum*
Psocus sp.	Neuroptera	*Gregarina psocorum*
Pterostichus stygicus (Say)	Coleoptera	*Gregarina intestinalis*
		Gregarina monarchia
Pterotrachea sp.	Mollusca	*Gregarina pterotracheae*
Reduvius personatus L.	Hemiptera	*Hyalospora reduvii*
Rhizotrogus aestivus Oliv.	Coleoptera	*Euspora fallax*
sp.	Coleoptera	*Actinocephalus stelliformis*
		Stictospora provincialis
Rhyacophila sp.	Neuroptera	*Asterophora mucronata*
Rhynchobolus americanus	Annelida	*Gregarina* sp. (Porter)

Host	Group	Parasite
Salpa aerginosa	Tunicata	*Gregarina ensiformis*
confoederata	Tunicata	*Gregarina flava*
maxima	Tunicata	*Gregarina salpae*
vagina	Tunicata	*Gregarina flava*
Scarabaeus relictus	Coleoptera	*Gregarina scarabaei*
Schistocerca americana Burm.	Orthoptera	*Gregarina rigida*
paranensis Burm.	Orthoptera	*Gregarina paranensis*
Schizophyllum corsicum Bröl.	Myriapoda	*Stenophora varians*
Sciara sp.	Diptera	*Actinocephalus caudatus*
Scolopendra cingulata (Latr.)	Myriapoda	*Nina gracilis*
		Actinocephalus striatus
heros Giard	Myriapoda	*Amphorocephalus amphorellus*
oraniensis	Myriapoda	*Nina giardi*
oraniensis lusitanica Verh.	Myriapoda	*Nina giardi corsicum*
subspinipes Leach	Myriapoda	*Nina indicia*
woodi Mein.	Myriapoda	*Hoplorhynchus scolopendras*
Scolopocryptops sexspinosus (Say)	Myriapoda	*Hoplorhynchus actinotus*
sp.	Myriapoda	*Hoplorhynchus actinotus*
Scutigera forceps (Raf.)	Myriapoda	*Trichorhynchus pulcher*
sp.	Myriapoda	*Trichorhynchus pulcher*
Sericostoma sp.	Neuroptera	*Taeniocystis truncata*
sp.	Coleoptera	*Ancyrophora uncinata*
Silpha laevigata F.	Coleoptera	*Actinocephalus acutispora*
thoracica L.		*Ancyrophora gracilis*
Sphingonotus sp.	Orthoptera	*Gregarina acridiorum*
Spirobolus sp.	Myriapoda	*Stenophora spiroboli*
spinigerus Wood	Myriapoda	*Stenophora larvata*
Statira unicolor Blanch.	Coleoptera	*Gregarina statirae*
Stigmatogaster gracilis Mein.	Myriapoda	*Rhopalonia geophili*
Strongylosomum italicum Latz.	Myriapoda	*Stenophora nematoides*
Talorchestia longicornis	Crustacea	*Frenzelina delphinia*
Tanypes sp.	Diptera	*Stylocystis praecox*
Tenebrio castaneus Knoch	Coleoptera	*Gregarina grisea*
molitor L.	Coleoptera	*Gregarina cuneata*
		Gregarina polymorpha
		Gregarina steini
		Steinina ovalis
Tenebrionidae	Coleoptera	*Gregarina tenebrionella*
Termes sp.	Neuroptera	*Gregarina termitis*
Thanasimus formicarius (L.)	Coleoptera	*Gregarina longirostris*
Timarcha tenebricosa (F.)	Coleoptera	*Gregarina munieri*
Tipula sp.	Diptera	*Gregarina longa*
sp.	Diptera	*Gregarina tipula*
sp.	Diptera	*Hirmocystis ventricosa*
sp.	Diptera	*Actinocephalus tipulae*

Host	Group	Parasite
Tribolium ferrugineum F	Coleoptera	*Gregarina minuta* *Steinina obconica* *Didymophyes minuta*
Triactylus variegatus Latr.	Orthoptera	*Gregarina hyalocephala*
Trox perlatus Scriba	Coleoptera	*Gregarina acuta*
Tryxalis sp.	Orthoptera	*Gregarina acridiorum*
Uca pugilator	Crustacea	*Frenzelina nigrofusca*
pugnax	Crustacea	*Frenzelina nigrofusca*
Udeopsylla nigra	Locustidae	*Gregarina udeopsyllae*
Xylopinus saperdioides Oliv.	Coleoptera	*Stylocephalus* sp.

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†Described in The Journal of Parasitology, 2:129-136.

*A preliminary description was given in The Journal of Parasitology, 2:27-36.

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EXPLANATIONS OF PLATES

All original drawings were made with the camera lucida directly from the live material and the magnification of each is given.

All the drawings which were copied from other authors were drawn by means of the camera lucida and the source of each drawing is given in the explanation of the individual plates. No magnifications are mentioned in the majority of the original sources and hence none can be given here.

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PLATE IV

PLATE V

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Fig. 107. *Stylocephalus longicollis* (Stein) Watson. After Schneider, 1875, Plate XIX, Fig. 1.

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Fig. 110. *Lophocephalus insignis* (Schneider) Labbé. After Schneider, 1882, Plate XIII, Fig. 1.

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Fig. 119. *Pyxinia rubecula* Hammerschmidt. After Frantzius, 1848, Plate VII, Group II, Fig. 1.

Fig 120. *Stylocephalus oblongatus* (Hammerschmidt) Watson. After Schneider, 1875, Plate XVIII, Fig. 5.

Fig. 121. *Stylocephalus longicollis* (Stein) Watson. After Schneider, 1875, Plate XIX, Fig. 2.

Fig. 122. *Ancyrophora gracilis* Léger. After Léger, 1892, Plate XIX, Fig. 11.

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PLATE V

PLATE VI

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Fig. 147. *Gregarina munieri* (Schneider) Labbé. After Schneider, 1875, Plate XVII, Fig. 1.

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PLATE VII

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PLATE VIII

PLATE IX

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Fig. 217. *Gregarina acuta* (Léger) Labbé. After Léger, 1892, Plate VI, Fig. 10.

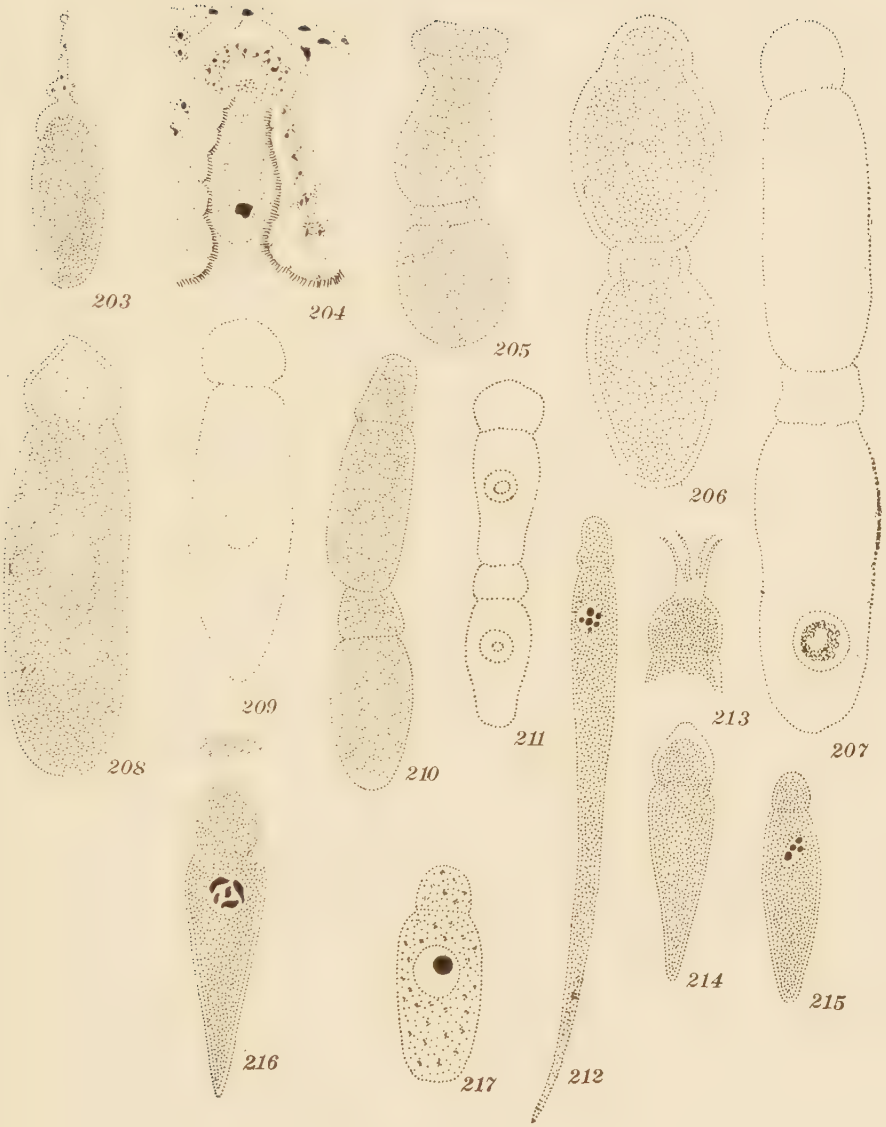

PLATE IX

PLATE X

EXPLANATION OF PLATE

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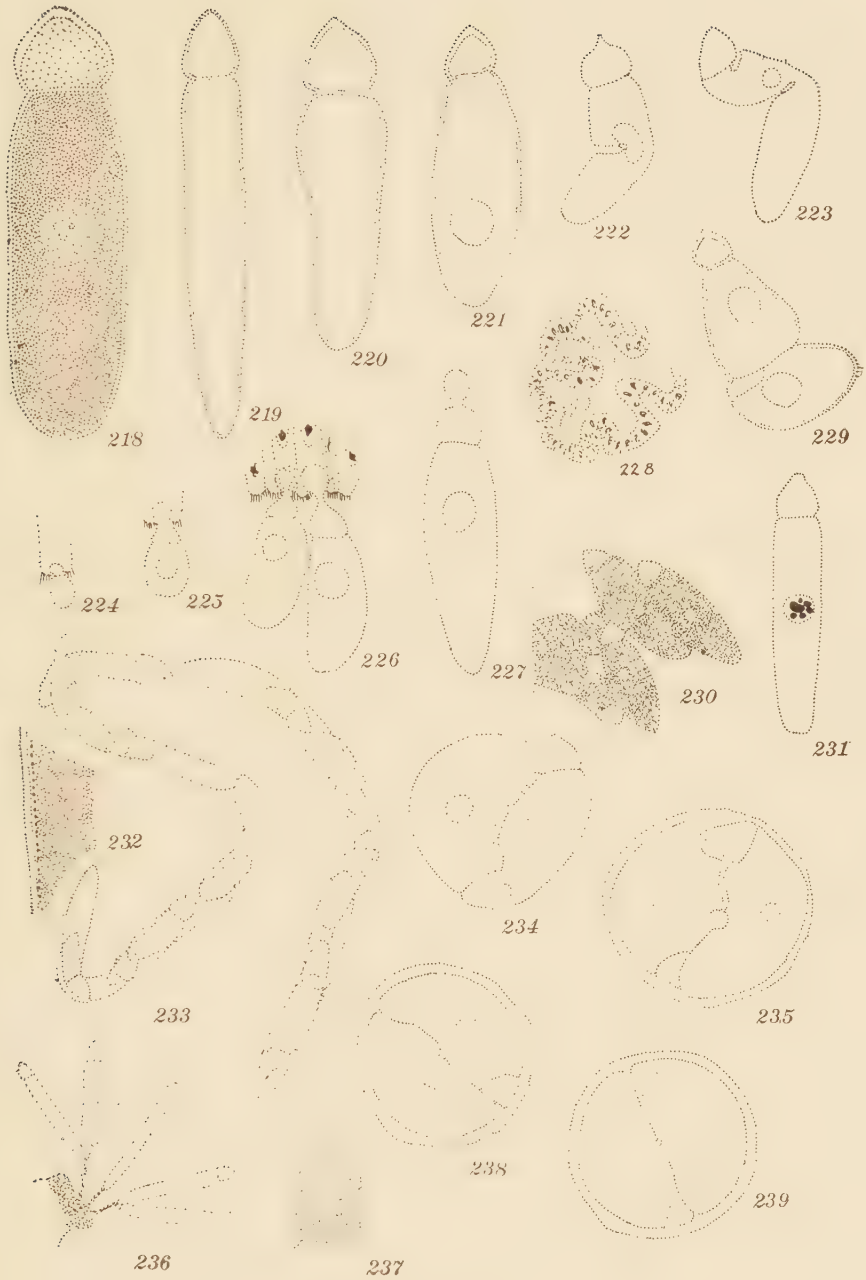
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PLATE X

PLATE XI

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Figures 240-255. *Leidyana erratica* (Crawley) Watson.

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PLATE XII

EXPLANATION OF PLATE

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PLATE XII

PLATE XIII

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Fig. 288. An association from a starved host, showing the concavity in the end of the primite. × 100.

Fig. 289. A trophozoite attached to the epithelial wall of the host. × 100.

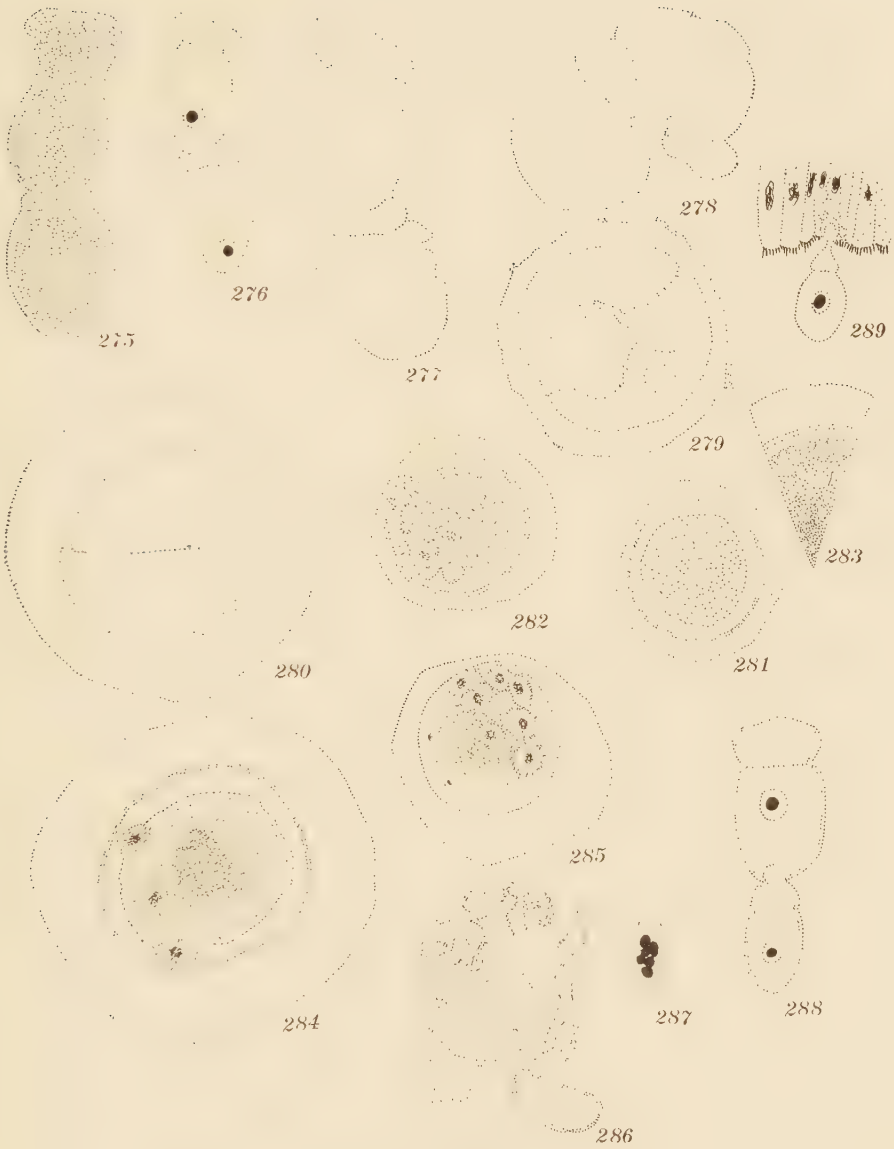

PLATE XIII

PLATE XIV

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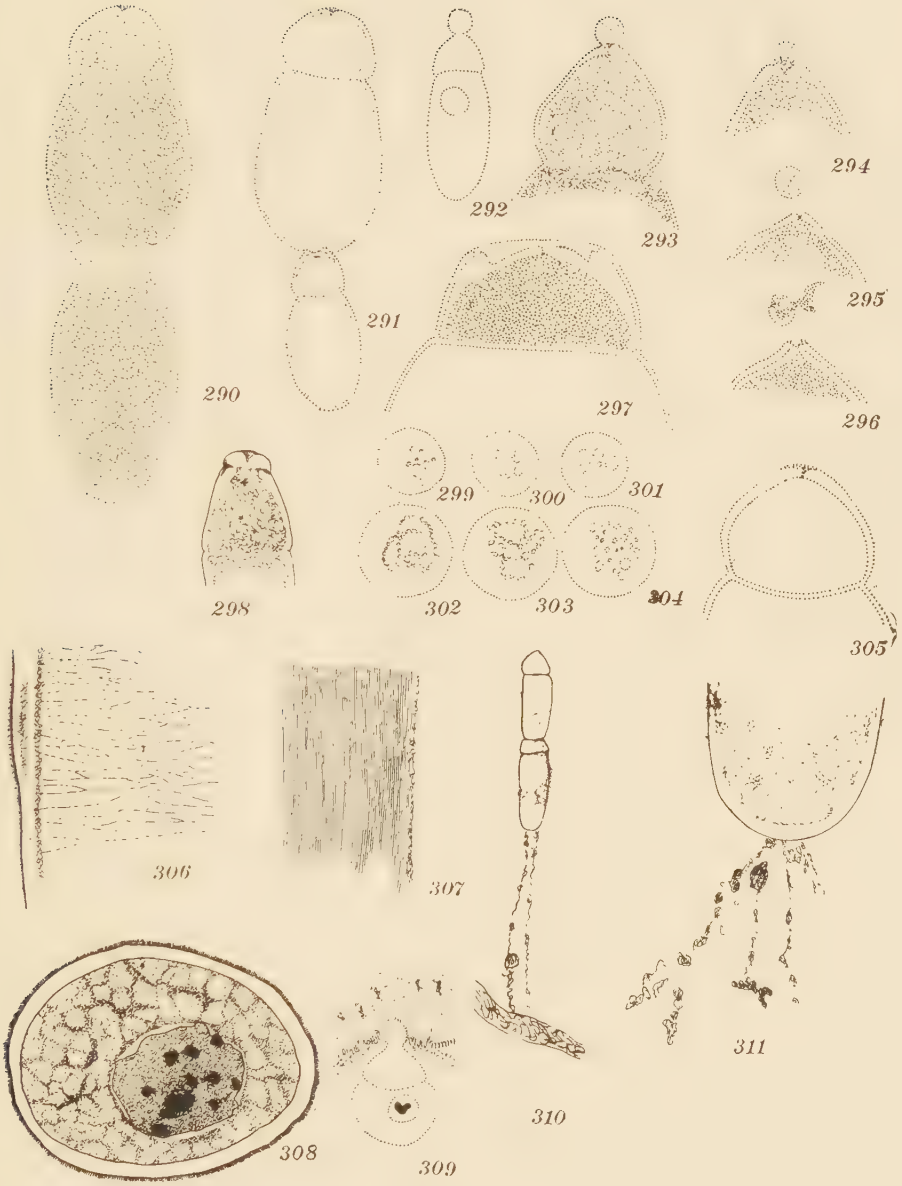
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PLATE XIV

PLATE XV

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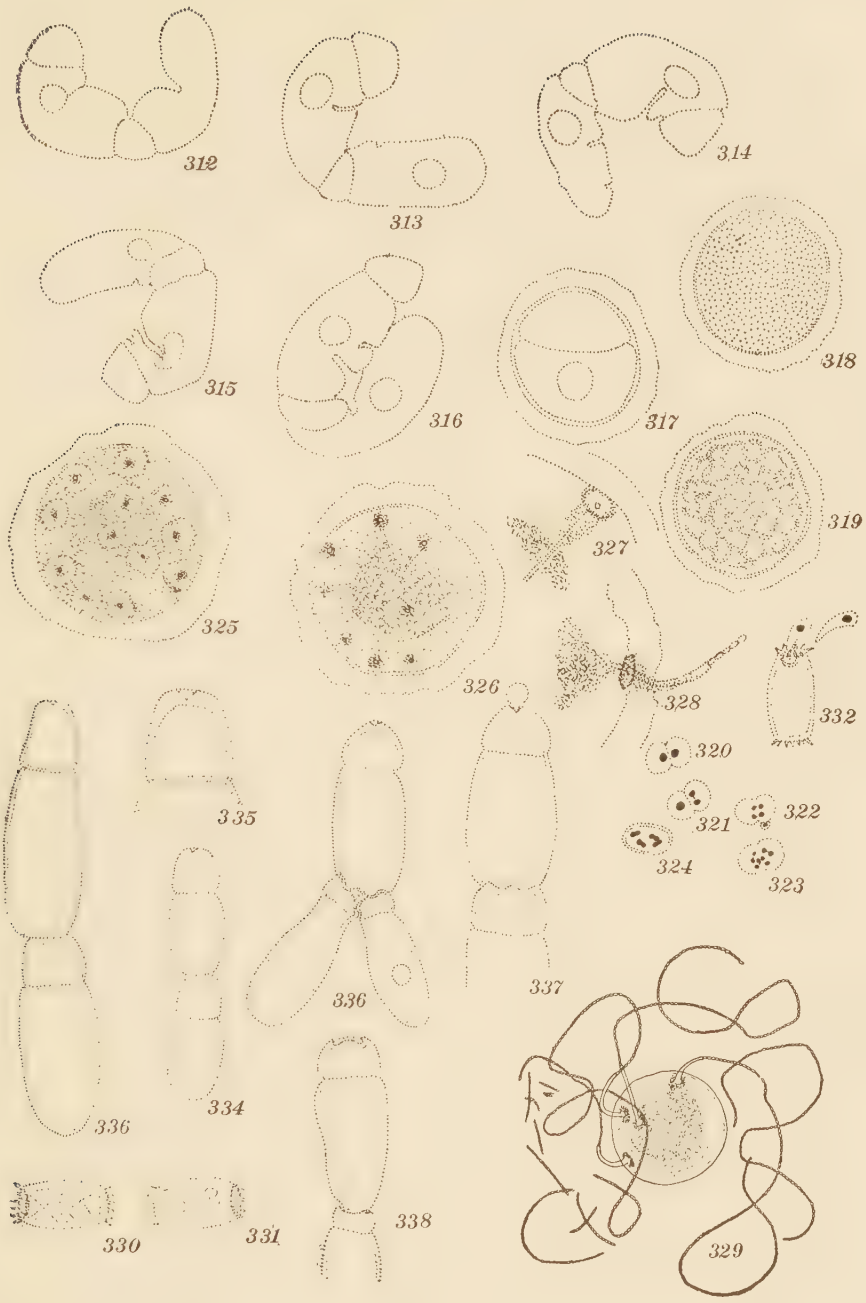
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PLATE XV

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Page 18	line 3	for	*mobüszi*, read *möbuszi*
25	25		0.8, read 0.8 micron
28	30		(Fig. 70), read (Fig. 10)
29	24		*Stenaphora*, read *Stenophora*
47	transfer		Genus 49 *above* Family 8 into Family 7
48	line 4	for	Ulvina, read Ulivina
48	21		*virginensis*, read *virginiensis*
48	24		*Julus boleti* C. Koch, read *Julus fallax* Meinert
48	32		*Brachydesmus*, read *Brachyiulus*
49	20		1913a:286, read 1913b:286
53	2		[Figure 6], read [Figures 5 and 6]
56	34		*julu*, read *juli*
60	22		FONTARIA, read FONTARIAE
60	24		1913:53, read 1903:53
60	26		*fontaria*, read *fontariae*
61	22		*fontaria*, read *fontariae*
64	31		Fabricus, read Fabricius
69	3		1912a:8-10, read 1912b:8-10
69	18		1912:681-5, read 1912a:681-5
69	30		*Orthomorpha coarctata*, read *Parajulus* sp.
70	3		1912:685-6, read 1912a:685-6
70	5		minimum 390 micra, read maximum 390 micra
80	35	after	*Scolopocryptops sexspinosus* insert *Scolopocryptops* sp.
81	7	for	1903:310-1, read 1903a:311
84	28		[Figure 32], read [Figures 32, 270, 272]
Page 90	line 1	for	STRIATIUS, read STRIATUS
94	19		*Oeipoda*, read *Oedipoda*
94	20		*migratoriae*, read *migratoria*
94	36		*Schistocera, read Schistocerca*
95	3		*atlanis*, read *atlantis*
95	10		*Schistocera*, read *Schistocerca*
95	30		(Diesing) Ellis, read (Diesing) Watson
96	23		Oedipda, read Oedipoda
97	27		1845:95, read 1848:194
97	34		1904:14-18, read 1904:64-87
98	1		:: 12, read :: 1 : 2
99	35		*Blattae*, read *Blatta*
100	34		*Dissosteria*, read *Dissosteira*
101	5		Stephanohora, read Stephanophora
102	25	insert	[Figure 199]
102	26	for	1875:674, read 1875:574
103	16		1892:290-300, read 1892:299-300
104	2		1893:811-13, read 1893a:811-13
104	33		1900:140-44, read 1900:40-44
108	14		*valgas*, read *valgus*
41	8		Stein, read Frantzius
68	28		*fontaria*, read *fontariae*
68	33		*fontaria*, read *fontariae*
106	8		*luridis*, read *luridus*
125	25		Stein, read Frantzius
143	11		Stein, read Frantzius